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UNIVERSITY OF ALBERTA

Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae and Ironomyiidae (Diptera: Phoridea)

by

Brian V. Brown ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Doctor of Philosophy

Department of Entomology

EDMONTON, ALBERTA

Spring 1991

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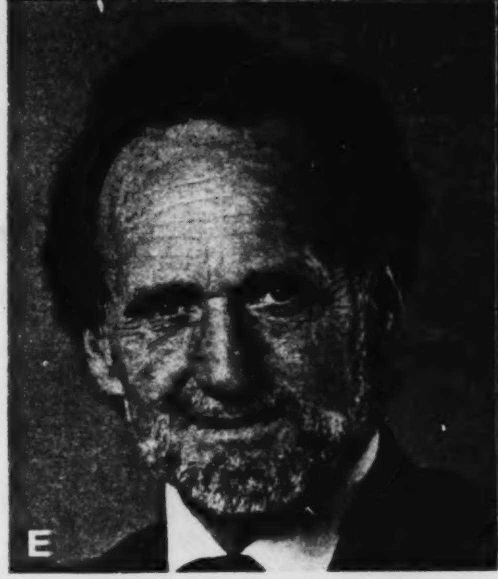
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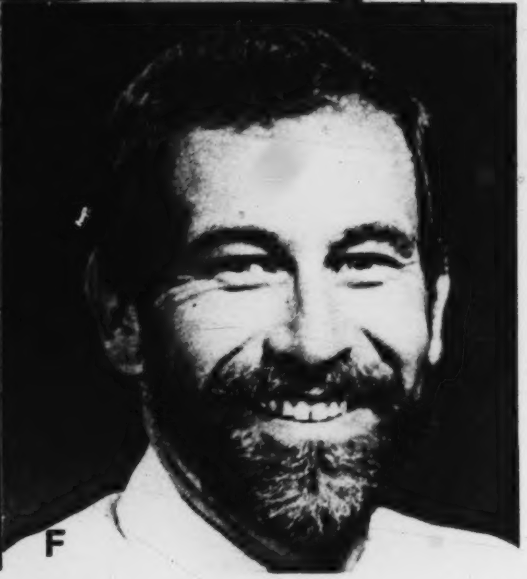
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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled: Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae and Ironomyiidae (Diptera: Phoridea), submitted by Brian V. Brown in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

The Phoridae is a little-studied family of small (1-6mm) flies with extremely divergent life histories. Most species have not been described yet, especially from tropical regions. The generic classification used for these flies during the last sixty years is no longer useful, as it clearly forms groups based on primitive character states, rather than on shared, derived character states.

The Nearctic Region genera of Phoridae are here revised, showing that the previous classification of these flies into three subfamilies was inadequate. The outgroups of the Phoridae are reviewed, showing that the most closely related taxa to the Phoridae are the Sciadoceridae and Ironomyiidae. Use of these outgroups to polarize character states in the Phoridae allows the re-organization of this family into 5 subfamilies, Hypocerinae, Phorinae, Aenigmatiinae, Conicerinae and Metopininae. The newly re-defined Phorinae is the adelphotaxon (sister-group) of the Aenigmatiinae + Conicerinae + Metopininae, among which the relationships are unknown. The hypocerines are the adelphotaxon of all other extant Phoridae. Within the Hypocerinae the relationships of the fifteen included world genera are hypothesized, and three new genera are proposed. The relationships of the six world phorine genera are insufficiently understood, and only partly resolved. The Aenigmatiinae is organized into two tribes, Aenigmatiini and Diplonevrini. The relationships of the seven world Diplonevrini are hypothesized, whereas those of the Aenigmatiini are not discussed. The six world conicerine genera are revised and relationships hypothesized. The

Metopininae is the largest group of Phoridae, with well over one-half of the named taxa. Two major groups are recognized, the *Metopina*-group and the *Megaselia*-group. *Beckerina* Malloch is the adelphotaxon of these two groups, whereas *Rhopica* Schmitz and *Triphleba* Rondani are successive outgroups of all metopinines. The *Metopina*-group is mostly tropical in distribution and is not discussed further. The *Megaselia*-group is partially organized into the *Gymnophora*-subgroup and the *Apocephalus*-subgroup. Species-level revisions of genera are needed before further progress can be made in this family, as the distribution of character states is insufficiently known. Genera in greatest need of revision include *Peromitra* Enderlein, *Chaetopleurophora* Schmitz, *Megaselia* Rondani, and *Apocephalus* Coquillett.

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1. Introduction

> I start my account of the family
> Phoridae on this macabre note, because
> this is a macabre family... (Oldroyd, 1964)

This study began as an attempt to organize the huge genus *Megaselia* Rondani into monophyletic taxa, so that progress could be made toward its proper classification. Early in my research, I realized that I could not accomplish my goal unless I knew the limits of other genera closely related to *Megaselia*, within the newly proposed *Megaselia*-group of genera (Disney, 1987). This process led to the conclusion that the entire family needed revision, a work that would provide a framework for studies like the one I first attempted.

The last revision of the family was the PhD thesis of the late Hermann Schmitz (Schmitz, 1929). A large number of species descriptions had accumulated, allowing Schmitz to propose a new grouping of genera into his six subfamilies. His arrangement served phoridology well, as within its framework he and the late Thomas Borgmeier described hundreds of phorid species and tens of genera. In the last twenty years, however, with the rise of cladistic techniques (Hennig, 1966) and the increasing numbers of unusual taxa discovered by Henry Disney, this classification outlived its usefulness. Disney (1983) became so disenchanted with the system that he declined to use it in his Handbook of British Phoridae. The time has become ripe for a new synthesis of phorid genera.

In this thesis I attempt to organize the genera of Phoridae from the Nearctic Region into monophyletic groups and provide a new classification. Specimens of genera from outside of the Nearctic Region, when available, were used to widen the coverage to the entire world fauna. First, I organize the outgroups of the Phoridae; then I establish the groundpattern character states and new subfamily classification for the group. A treatment of each subfamily follows, with the constituent taxa revised and classified, if possible. Each of Chapters 2-8 is intended to be a manuscript for a separate publication.

The Phoridae are a fascinating, unappreciated group of insects, the divergent life histories and ecological importance of which deserve further study. Hopefully this work will provide a framework for such studies, and stimulate further research on the taxonomic aspects of these flies.

1.1 General characterization

The family Phoridae is a monophyletic group of small (1.0-6.0 mm) flies that are found worldwide. There are approximately 3000 described species in 250 genera, but this is an extreme under-representation of the true world fauna, that probably exceeds 10000 or more species. Generally regarded as scavengers, saprophages and "garbage feeders", phorids have a reputation for unwholesome ways of life. Oldroyd (1964) described them as a "macabre family" and gave them the common name coffin flies, because of the habits of one species, *Conicera tibialis* Schmitz, that breeds in corpses.

Many German researchers called phorids running flies because adults of some genera are frequently seen running on leaves. In North America, the most often used common name is humpbacked flies, referring to the enlarged thorax. Recently, a British worker, R.H.L. Disney, has introduced the name scuttle flies for the group, referring to their distinctive running style.

1.2 Recent phorid workers

To understand how the study of phorids has progressed, or not progressed, it is useful to review the history of students of this family. Although many dipterists have described a few phorid species (see Schmitz, 1929 for a review of earlier workers), the most important workers on the Phoridae in this century were Thomas Borgmeier (1892-1975) and Hermann Schmitz (1877-1960), whose lives and works have been summarized fully (Borgmeier, 1971a; Kempf, 1976; Mannheims, 1963; Schmitz, 1928, 1940; Wirth *et al.*, 1978). Other workers who made significant contributions to phorid taxonomy in the early part of this century include Charles Thomas Brues (1879-1955, Melander, 1955), Charles N. Colyer (1908-1970, Smith, 1972), William Lundbeck (1863-1941, Kryger, 1942), and John Russell Malloch (1875-1963, Sabrosky, 1963). After the deaths of Borgmeier and Schmitz, however, a hiatus occurred where little taxonomic research on Phoridae occurred. Their disciples were unsuccessful in filling this gap: Borgmeier's protegé, Angelo Pires do Prado, published only two papers about Phoridae (Borgmeier & Prado, 1975; Prado, 1976); Schmitz' students A.

Bridarolli and Erwin Mathias Beyer did somewhat better (Bridarolli wrote 9 papers, Beyer 25 papers, see Borgmeier, 1968, 1971b), but did not meet the same standard of excellence as their mentor. The next group of phorid taxonomists to emerge includes the current workers: Jeffrey K. Barnes, R. Henry L. Disney, and me. Two recent workers, Tadao Gotô and William H. Robinson, have found employment in other fields of entomology and no longer work on phorids, while one further enthusiast, Hugh Oliver, is employed currently in other work but hopes to research phorid taxonomy in the future. Finally, detailed investigations of ant-phorid host-parasite interactions are being made by Donald Holt Feener, Jr.

1.3 Way of life of Phoridae

1.3.1 Natural History

In spite of their reputation as generalized scavengers, developing in decaying vegetation, dung and carrion, recent studies summarized by Disney (1979, 1990b) and Ferrar (1987) have shown that life histories of phorid flies are extremely divergent. Many are specialized predators, and various species have been recorded eating slug eggs, caddisfly eggs, spider eggs, sciarid (Diptera) larvae, cecidomyiid (Diptera) larvae, gall-forming and root aphids, violet seeds and living fungi. Many others, as larvae, are parasitoids or symbionts of social insects, especially termites and army ants, but also bees, wasps and myriapods. Finally, there are numerous species that feed as larvae in decaying material, some of which develop only in specific media such as fungi or dead snails, but others that can develop successfully in any organic medium.

The most polyphagous phorid known is *Megaselia scalaris* (Loew), which breeds in decaying vegetation, carrion (including human corpses), dung, milk, dead insects, blood engorged female ticks, human gut tract, urogenital tract and eye, frog eggs, bee colonies and even boot polish (Robinson, 1971). The entire range of larval food is summarized well by Ferrar (1987), and need not be repeated here.

While taxonomic studies of the group are proceeding (see Borgmeier, 1968, 1971b; Brown, 1990a for most of the relevant literature), and life history data are reported sporadically, research on the immature stages and behavior of the group are lagging far behind. Few larvae have been described, for instance, and immature stages of almost all phorids currently are unrecognizable. Some recent authors, however, have examined the structure and behavior of adult and larval phorids and have made many fascinating discoveries, some of which are summarized below.

1.3.2 Mating behavior

Like other aspects of phorid behavior, mating behavior is little known for most species. Prior to copulation in *Gymnophora luteiventris* Schmitz, there seems to be little interaction, as a male simply leaps on a female (Brown, 1985). This lack of foreplay has been observed also in *Phalacrotophora halictorum* (Melander and Brues) (Wcislo, personal communication), but there is extensive courtship in *Megaselia scalaris*, involving wing and leg movements (Miller, 1978). Females of all of the above mentioned species, as well as *Puliciphora* (see below) are known to mate more than once.

In the most detailed examination of phorid mating behavior, Miller (1978, 1984) found no courtship in *Puliciphora borinquenensis* (Wheeler). Instead, males and apterous females usually came together at the larval food source, decaying organic material. Since males do not feed, and live only for 2-3 days (as opposed to females, that feed and live for 2-3 weeks), they are definitely attracted to these sites for mating. Males mounted females, shook violently from side-to-side, and either inserted their genitalia or were rejected. If successful in inserting its genitalia, a male periodically stroked the head and thorax of the female during copulation. Finally, near the end of copulation, the male swung from side to side laterally several times, pivoting on his genitalia, and then discontinued the copulation. In crowded conditions female *Puliciphora* spread out from the food source and assumed a characteristic head-downward stance on the sides of their enclosure cages. During this time, the dorsal flap of the abdominal glands was observed to be open and the abdomen showed vigorous pumping movements, indicating that perhaps a pheromone was being released. These females were said to be "parading". Males of this species performed four different reproductive routines in the experiment, labeled A1, A2, B1 and B2. "A" routines involved stationary (on the ground) copulation while "B" routines involved copulation in flight. The mechanics of these routines were as follows:

A1 - males rapidly copulate with many (up to 0.66 per minute) of the parading females on the ground.

A2 - males wait at oviposition sites for non-parading females to arrive, and copulate with them.

B1 - males pick up and carry a parading female *in copula* (all females are wingless) to an oviposition site.

B2 - males pick up and carry a parading female *in copula* to a random location.

Males apparently learn the location of oviposition sites and thus are able to transport many (up to 0.5 per minute) females to a new site. Once the male released the female following a B routine, he followed her closely for up to 10 seconds, which Miller regarded as non-contact guarding behavior, to prevent females from mating again. Males persisted with an A or B routine for long periods of time, but were able to switch between them. Older males used B routines much more than younger males did, but both used A routines more than B routines. There is probably a greater chance for the offspring of a B routine to develop, but there is obviously a much greater energy cost to males. Indeed, flight in the copulating pair seemed "slow and heavy" and in some instances females were too heavy for males to lift off the ground.

Binns (1980) studied mating behavior of *Megaselia halterata* (Wood), a fly that causes economic injury to commercially grown mushrooms. He found that males performed a "gyrating run" display that consisted of rapid movement in tight circles, with waving and trailing of the wings. Often, several males performed this display in front of a female, and there was competition among males to copulate with her. Many females stood with the abdomen outstretched, which Binns believed indicated they were disseminating a pheromone. The paired flies often flew *in copula*.

Males of many phorid species are known to form swarms on leaves (e.g. *Phora velutina* Meigen, Colyer, 1954, *Burmophora* Beyer, Gotô, 1983, *Dohrniphora maddisoni* Disney, Disney, 1990a) or in the air, under tree limbs (*Phora* spp, personal observation, Gotô, 1984). Sivinski (1988) described all-female swarms of *Megaselia aurea* (Aldrich) and *Rhyncophoromyia conica* (Malloch), as well as all-male swarms of the latter. Females of *M. aurea* scurried in milling groups on leaves and occasionally were pounced upon by males. The pair immediately took flight, usually with no courtship having been observed. One male, however, buzzed its wings at a female before mounting her and taking flight. This is a reversal of sexual roles that normally occur, where males swarm and females selectively enter the swarm to select mates. It raises the possibility that males of these two species provide some kind of energetic or nutritional investment to reproduction that makes them valuable to females (Sivinski, 1988).

Finally, W. Wcislo (personal communication) observed that males of *Phalacrotophora halictorum* (Melander and Brues), a parasite of halictid bee larvae, mounted females without preliminary courtship. The male immediately inserted his genitalia and the pair took flight *in copula*. During the first half of the copulation, the male drummed the head and thorax of the female with his front legs, and in the second half, the female rapidly shook her abdomen, apparently in an effort to dislodge the male. Females were observed to mate more than once.

1.3.3 Oviposition behavior

The most striking female oviposition behavior is found in females of parasitic genera, such as *Apocephalus*, *Pseudacteon*, *Plastophora*, and others. Feener (1981, 1987, 1988) and Feener and Moss (1990) have described the social effects of such parasitoids on their ant victims, and incidentally phorid oviposition behavior. *Apocephalus feeneri* Disney preferentially attacks soldiers of *Pheidole dentata* Mayr (Feener, 1981), possibly because of the enlarged head of this caste. The phorid hovers over the colony, darting occasionally at the soldiers. Similar behavior is found in *Pseudacteon crawfordi* Coquillett, that attacks *Solenopsis* spp. (Formicidae) (Feener, 1987; personal observation). Observations were made on ants that were attracted in large numbers to canned tuna fish baits. Most workers rear up in a distinctive defensive posture, with jaws gaping and mandibles gnashing at the flies hovering about one centimeter out of reach, but a small number actually forage on the bait. Occasionally, a fly is able to land, undetected, on one of these foraging ants, and oviposit between the ant's thoracic sclerites. The ant is completely oblivious to the fly's presence, but flinches violently at the oviposition event.

Parasitoids of the ant genus *Atta* recently have been studied (Feener & Moss, 1990; Feener and Brown, in manuscript), and are of great interest, as their ant hosts are economically important in Neotropical agriculture. Feener and Moss found that phorid flies, *Apocephalus attophilus* (Borgmeier), are responsible for the "hitchhiking" behavior found in *Atta columbica* Guerin. "Hitchhikers" are small workers that ride back to the colony on a leaf fragment carried by larger workers. They protect the leaf carriers by chasing away female *A. attophilus* that land on the leaves and attempt to oviposit in the mandibular suture of the ants. Since the flies apparently need to land on the leaf to deposit an egg, the hitchhikers can be effective deterrents when they are present. Adult females of *Neodohrniphora curvinervis* (Malloch), however, have no need to land on leaves, and do not attack leaf carriers of *Atta cephalotes* (L.) (Feener & Brown, in manuscript). Instead, females take up vantage points on the leaves of undergrowth plants over foraging columns of ants, and sally out after appropriate-sized, outbound workers. A fly hovers over an ant, following its movements closely, and suddenly darts down to land on the ant's head, facing forward. The fly then thrusts her ovipositor through the suture of the occipital foramen, at the back of the ant's head, and injects an egg.

Females of two species of *Diplonevra* described by Disney (1986b) from Sulawesi exhibit complex pre-ovipositional behavior. When termite nests were broken open, phorids were attracted, including females of these two species. A female phorid runs up to a worker termite and prods it from behind with its head. The worker immediately chases the fly, (spurred on by the presence of an odor produced by the fly, according to Disney), but if its interest flags, the female again runs behind and butts the worker. After luring a termite away from the nest, a phorid somehow (not observed by Disney) renders it "comatose", wraps it in soil particles, lays an egg on it and stands guard on top.

Banks (1911) observed adults of *Plastophora juli* Brues (below reclassified as *Myriophora juli* (Brues)) darting around a fleeing myriapod. A similar attack was observed on an injured *Pachycondyla impressa* (Roger) (Formicidae) in a montane forest near Tinalandia, Ecuador (personal observation). This ant, which could barely walk (it had only three legs), had three *Apocephalus* females running around on, but never leaving, its body. Additionally, other phorid parasitoids of injured ants are now known (Brown & Feener, in press-a, b; Disney & Schroth, 1989).

Detailed observations on a phorid fly (as yet unidentified to genus) attracted to injured ants were made in moist, semi-evergreen forest at Khao Yai National Park, Thailand. Flies were attracted to a large range of experimentally crushed individuals of *Camponotus* spp. and *Camponotus*-like ants, but not to other ants such as *Oecophylla*. Pairs of phorids arrived at the ants *in copula*, but uncoupled immediately, with the male departing at once. Females landed on the ants and probed their bodies extensively with their mouthparts. Gradually, the fly moved toward the head and probed in the area of the antennal socket. Upon reaching this structure, the fly reversed its position and inserted its ovipositor into the antennal socket, apparently laying a single egg. After ovipositing, the fly again reversed its position and appeared to feed on fluid at the oviposition wound, as do females of *Apocephalus paraponerae* (Brown & Feener, in press-b). Several seconds later, the fly reversed its position and inserted its ovipositor again for a short period of time, then turned back to feed. Apparently this pseudo-oviposition takes place to encourage the flow of body fluids through the oviposition wound. More than twenty cycles of alternating pseudo-oviposition and feeding were observed for some individual flies. Other individual flies of the same species pseudo-oviposited and fed at oviposition wounds, but it is unlikely that they oviposited in them, as only one larva was reared from each ant, even though several flies may have visited the body. Also, only relatively brief pseudo-ovipositions were observed after the first fly completed the lengthier true oviposition. It is likely some kind of oviposition marker pheromone is deposited by the first fly. Undamaged ants, which were often present in large numbers nearby, were not attacked by these phorids.

1.3.4 Immature stages

The immature stages of phorids, like their life histories, are incompletely known. Ferrar (1987), Hennig (1952), Keilin (1911) and Schmitz (1938, 1941) are the major references. Whitten (1955) described the tracheal system of the larva of a species of *Megaselia*. Recently, the larvae of some predatory and parasitic species have been described (Brown & Feener, in press-b; Brown *et al.*, in press; Robinson & Brown, in manuscript) with particular reference to characters of potential phylogenetic importance: the presence of an interantennal papilla, structure of the cephalopharyngeal skeleton, presence of sclerites on the thorax and abdomen, presence of patches of spines, form of the anterior and posterior spiracles. Much work remains to be done on immature stages of Phoridae.

1.3.5 Development

Phorid development has not been studied extensively. Usually, the only information available is the amount of time spent in the larval and pupal stages. Thus, individuals of *Gymnophora luteiventris* were found to spend about 10 days as a larva and 15 days in the puparium (Brown, 1985). *Megaselia scalaris* developed from egg to adult in approximately 21 days according to Benner and Ostermeyer (1980), who also noted that adult males eclosed 4 days earlier than females and that the sex ratio of the adults emerging were skewed towards males. A more complete review of the life history parameters of some Phoridae is given by Brown and Feener (in press-b).

Robinson and Foote (1968) reported on the natural history of *Megaselia aequalis* (Wood), a predator on eggs of slugs of the species *Deroceras laeve* (Müller). The first larval instar lasted one or two days and larvae fed only on the perivitelline membrane of the slug egg. After molting to the second instar (still inside the slug egg), larvae continued feeding, this time attacking the slug embryo. After two days larvae left the egg, molted to the third instar and re-entered the egg. At first, third instar larvae fed only upon the gelatinous matrix in which the slug eggs were laid, but after about one day they attacked and ate several more embryos. This stage lasted 3-5 days after which larvae pupated for ten to fifteen days. The overwintering stage is the puparium.

Finally, in Termitoxeniinae, the free living larval period is very short, lasting only a few minutes in one species and up to several hours in others (Borgmeier, 1964a).

1.4 Material

This revision is based on the study of several thousand phorid specimens, not all of that are listed in the following chapters. Many were collected during my tenure at the University of Guelph, whereas others were gathered at home or on field trips while at the University of Alberta. Some specimens, mostly those of taxa that are known from few specimens or those from outside of the Nearctic Region, were borrowed from institutions listed below. The name of each institution is preceded by a coden (for example CNC), used as an abbreviation in the lists of material examined. The names of museum curators are in parentheses.

BVB - collection of the author.

CNC - Biosystematics Research Centre, Agriculture Canada, Central Experimental Farm, Ottawa, Ontario, Canada, K1A 0C6 (J.M. Cumming).

HO - collection of Hugh Oliver, Plant Protection Group, Ruakura Agricultural Station, Private Bag, Hamilton, New Zealand.

USNM - United States National Museum, Smithsonian Institution, Washington, DC, USA, 20560 (F.C.Thompson).

ZFMK - Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 150-164, D-5300, Bonn 1, Germany (H. Ulrich).

1.5 Methods

1.5.1 Collecting Techniques

Collecting phorid flies is an inexact, and often frustrating pursuit. It is important to optimize collecting methods in order to be able to get a reasonably representative sample of the fauna, especially when on expeditions to remote or distant areas. Cost per specimen can be minimized and rarely collected species can be obtained. Unfortunately, collecting methods have received little attention, partly because almost any technique will catch some Phoridae, but no doubt largely because there are already vast numbers of phorid specimens that represent new species and genera in the insect collections of the world. Further collecting is necessary and justified, however, because most species are represented by only one or a few specimens. Large numbers of specimens are necessary, not only to supply adequate series for dissections and observation of variation, but because samples with large numbers of specimens invariably contain a few of the most rarely collected taxa. Many new species still await collecting even in "well collected" areas; in less well-known areas, many species are being destroyed daily with the human destruction of forests of the world. Particular attention needs to be paid to collecting specimens of Phoridae (and other insects) in the tropical forests that are being eliminated at an appalling rate worldwide; some areas especially worthy of attention are noted by the National Research Council (1980).

Summaries of collecting methods for Phoridae are few, although a short discussion on this subject is given by Disney (1983). According to Borgmeier (1964b), species of *Megaselia* are most easily collected by "sweeping the net (without meshes) on wet places between bushes and in low herbage". In a more comprehensive study, Disney *et* *al.* (1982) experimented with various trapping methods in an attemped faunal survey of Diptera in England. This study, conducted over a single week at the well studied Malham Tarn Nature Reserve, compared the collecting results of Malaise traps, pitfall traps and different colored pan-traps. Their conclusions were that Malaise traps and white pan-traps were the most efficient at collecting phorids, and that each sampled the fauna differently.

The study of Disney *et al.* (1982) mirrors my own (unpublished) results from comparisons of Malaise traps and flight-intercept-traps (FITs) (Masner & Goulet, 1981), used over a one-summer period at the University of Guelph Arboretum, Ontario. Malaise traps greatly outcollected FITs with respect to both numbers of taxa and numbers of specimens, but some species of *Megaselia* were collected only by, or in greater numbers by FITs. Placing pans under the center baffle of Malaise traps, as suggested by Marshall (1982), produced catches similar to those in FITs, but were generally greatly inferior to the catch from the head of the Malaise trap. Apparently, most phorid flies are negatively geotropic when they encounter a barrier (Girard *et al.*, 1972), and invariably run upward in a trap, unlike some other Diptera, such as Sphaeroceridae, that tend to move downward (Marshall, personal communication). Malaise traps run "dry"- that is with a strip of Vapona (Trademark) or cyanide as a killing agent- are far inferior to traps run "wet", with 70% alcohol as a killing and preservation agent.

There are instances, however, where Malaise traps are not the best devices for collecting phorid flies. In dry areas, such as dry oak/ pine forests in southern Arizona, especially during the driest seasons, water-filled pan-traps are superior to Malaise traps. During the hot part of the day, there is virtually no insect activity in these areas, but at cooler times (morning and evening) insects are drawn strongly to these traps and attempt to drink from them. Steep-sided pan traps, half-filled with water and a few drops of dish-washing detergent to break the surface tension, capture large numbers of specimens under these conditions. These pans can be effective also in non-arid areas when it has been a long time since the last rainfall. An example is a two-day collection from the foothills of the Rocky Mountains in Alberta, Canada, where a Malaise trap collected only a few specimens of common *Megaselia*, while 5 nearby yellow pan-traps yielded several specimens of the much less frequently collected genus *Gymnophora*. Generally, however, Malaise traps are more effective than pan-traps in non-arid areas.

Placement of Malaise traps is critical for collecting large numbers of phorid flies, but unfortunately, our knowledge of optimal placement for these traps is incomplete. Usually (*i.e.* Townes, 1972) it is recommended that Malaise traps be placed at a forest edge, with the back of the trap facing the dark forest and the front of the trap facing the field or other opening. Site differences were observed between three Malaise traps, run for 2 summers at the University of Guelph Arboretum in 1984 and 1985. One trap was at a forest/ field edge, one inside a mixed deciduous forest and one in a marshy meadow; as predicted the forest edge trap collected the largest number of specimens and taxa. This pattern was not repeated in a tropical forest, however, where presumably more factors come into play. Eight Malaise traps have been operated at the

La Selva Biological Station, Heredia, Costa Rica, in an attempt to sample phorid diversity. These traps were run in a number of situations: two in second-growth type forest, one in a natural treefall gap and five in primary rain forest. Most of these traps collected 20-100 phorids per week, but one primary forest trap collected approximately 1000 phorids per week. Similar collections have been made by some other collectors in tropical America, but the reason why some trap locations are far superior to others is unknown. Possibly humidity is more of a limiting factor in tropical forests, and in drier sites such as treefall gaps there is less phorid activity. The treefall gap site at La Selva, for instance, was certainly the richest for Coleoptera and some Hymenoptera, but was easily the least productive site for phorids.

A final variable for the successful use of Malaise traps is the period of time over which they are operated. Traps must be operated over as long a period as possible, preferably several years, in order to obtain something approaching a complete representation of the fauna. For example, although Malaise traps were operated for three years at the University of Guelph Arboretum, including two traps at the same spot for two years each, many phorid taxa were collected only once, or only in one year or one trap. In 1985, the diversity of genera collected was greater than in the previous years, but two genera collected in 1984 were not represented. Similarly, there were many taxa collected only once or at one trap among the 8 Malaise traps operated at La Selva. Presumably, further trapping would yield many more taxa.

Disney (1983, 1986a) criticised the use of Malaise traps because they collect too many other insects, making the sample "tiresome" to sort out, and suggested white bowl traps an alternative, producing good catches for little collecting effort. The objection to excessive time spent sorting can be overcome by using a system of screens to separate mechanically the preserved sample, removing all of the large and medium sized insects. The small fraction then can be sorted much more easily and efficiently. The use of bowl traps instead of Malaise traps, while convenient, is impractical in many field situations, as bowl traps should be cleaned out every day (especially in tropical climates), water must be present at the site or carried in, and traps must be protected from torrential downpours that quickly flood and empty them of their contents. Malaise traps, on the other hand, can be left for up to one month (depending on the number of insects collected and the size of the collecting vessel), need only enough liquid to fill the collecting bottle, and are unaffected by rain. The drawbacks of Malaise traps are their attractiveness to vandals and thieves, and their relatively high cost of construction or purchase (approximately $150 each). Bowl traps also can operate for long periods of time when ethylene glycol and soapy water are used as a collecting fluid, but many specimens thus collected are brittle and difficult to work with.

Although Malaise traps are in my opinion the most effective and convenient collecting tools for general sampling of phorid flies, other methods are more useful for specific taxa. A large number of phorid species are parasitoids of ants but are collected only infrequently with their hosts or rarely in Malaise traps. These flies usually are not present around normally functioning ant colonies, but appear at times when many ants are available as hosts, such as when workers of two colonies are fighting. One method for the attraction and collection of these ant-parasitoids was described by Williams *et al.* (1973), in their studies on fire ants (*Solenopsis saevissima* complex). They disturbed ant nests with a shovel to get large numbers of workers on the surface of the soil, attracting greater numbers of parasitoids. The success of their method is demonstrated by the results obtained: disturbed ant nests attracted 300 phorids in 10 hours of observation (1 fly per 2.1 minutes), whereas undisturbed nests attracted only 16 phorids in approximately 4.4 hours of observation (1 fly per 16.5 minutes). Feener (1981), in his studies on foraging behavior and competition in ants, discovered another way to attract phorid flies: baiting the host ants with canned tuna fish to attract large numbers of worker ants. This method was a great advance over the method of Williams *et al.*, as the actual ant nest need not be located, the stimulus for the ants to appear could be sustained over a longer period, and ants that are less aggressive than *Solenopsis* could be coaxed out of their nests. Other ant researchers also have collected or observed phorid flies using ant bait stations (Burges, 1979; Williams & Banks, 1987).

Phorids attacking or associated with ants that are not attracted to tuna baits must be collected by observing the ants during their normal activity, for example by watching foraging columns of leaf-cutter ants and army ants, by digging up the ant nest, or by deliberately injuring some workers. The last technique is effective only in certain instances where olfaction is used by phorids as a major cue to locate their hosts. An example is *Apocephalus paraponerae* Borgmeier, a phorid attracted to injured giant tropical ants *Paraponera clavata* (Fabricius) in South and Central America (Brown &

Feener, in press-a). Similarly, injured millipedes attract large numbers of some phorids.

Other techniques that may be effective are sweeping (which usually produces damaged specimens), and soil or leaf-litter extraction techniques (a highly successful method is given by Adis, 1987). Many adults, especially of the genera *Phora*, *Gymnophora*, and *Megaselia* in the Nearctic Region, can be hand collected as they run in their characteristic jerky manner on damp soil, on leaves in undergrowth, or in leaf litter. Males of the genera *Phora* and *Burmophora* often can be collected as they hover in swarms under large tree branches in forests (Gotô, 1984; personal observation) or over low plants (Gotô, 1983), respectively. Finally, light traps (Baumann, 1977; Khalaf, 1971), and emergence traps (Baumann, 1976, 1979; Disney, 1980; Disney & Gunn, 1980; Disney *et al.*, 1981; Weber & Prescher, 1990) have been used successfully to collect adults. Light traps are particularly useful for collecting myrmecophilous species (personal observation in Arizona and Costa Rica). Myrmecophilous Diapriidae (Hymenoptera) are attracted to blacklights placed near army ant bivouacs (L. Masner, personal communication), a technique that should be equally effective for collecting ecitophilous Phoridae, but with which I have not experimented.

Collecting larvae and pupae is much more difficult, and depends upon finding the larval food source. Usually, immature stages are stumbled upon by workers investigating other problems. Obvious places to look include fungi, insect, slug and spider eggs, the brood chambers of ant nests known to harbour commensal phorids, and the bodies of individual ants attacked by parasitic flies. Bringing fungi into the laboratory and rearing phorids from them in an enclosed container can be especially productive. Larvae of many species, such as species of *Gymnophora* (Brown, 1987), *Apocephalus paraponerae* (Brown & Feener, in press-b) and scavengers like many *Puliciphora* and *Rhynchomicropteron* species (personal observation) are reared easily in the laboratory in small petri plates with appropriate food and high humidity.

There is a seasonal aspect of phorid activity, making collecting efforts through all but the coldest months of the year necessary. A great number of relatively primitive, univoltine phorids are collected only in the early spring in the temperate zone; for instance, in southern Ontario and central Alberta, two sites with which I have experience, a typical collecting year starts as soon as the snow is mostly melted, early in the spring. Early season taxa such as some species of *Anevrina*, *Chaetopleurophora*, *Hypocera*, *Kerophora*, *Phora* and *Triphleba* are caught at this time. In early to late summer, adults of other genera become active, especially *Diplonevra*, *Dohrniphora*, *Gymnophora*, *Phalacrotophora*, and the ant associated genera: *Aenigmatias*, *Apocephalus*, *Rhyncophoromyia*, and others. In the fall, often even after the first frost, different species of *Triphleba* are collected. Species of *Megaselia* are found throughout the year, although there is a rise in the number of specimens collected in the fall in Ontario. In contrast, adult phorid activity is found throughout the year in tropical regions, but individuals of some species are active only during the wet (Feener, 1988; Ramírez, 1984) or dry (Feener & Moss, 1990) seasons.

1.5.2 Preservation and mounting

Phorid flies should be killed and preserved with 70% alcohol. Specimens killed with cyanide and allowed to air-dry collapse, become distorted, and because of their extreme brittleness, must be humidified before dissections can be made. Specimens collected in alcohol and critical-point-dried do not collapse and retain a limited flexibility such that the abdomen can be removed without humidifying the specimen. Another drying process using a commercially available chemical also works well (Brown, 1990b). When collecting small taxa, such as the genera *Pseudacteon*, *Puliciphora*, *Ecitomyia*, *Adelopteromyia*, *Chonocephalus* and others, it may be better to use 50% alcohol to prevent shrinking.

After critical-point-drying, I glue specimens to the sides of #2 insect pins with water-soluble white glue. Borgmeier (1963) strongly advocated micro-pinning phorid specimens, refering to mounting with glue as a "vicious method". Specimens glued to pins, however, are easier to dissect (an activity little practised by Borgmeier) because they are anchored more solidly to the pins. Also, it is much less time consuming to mount large numbers of specimens by glueing, especially when cardboard points are not used.

1.5.3 Dissection

For closer study some specimens were slide-mounted following the method of

Disney (1983), but I do not treat specimens this way routinely. Slide-mounted specimens offer only a limited view of important structures, such as male terminalia, that should be examined by further dissections, and by viewing from many angles.

Specimens in amber can be observed most clearly by immersing them in mineral oil. This serves to minimize the distortion caused by rough surfaces, as mineral oil has a refractive index similar to that of amber (Larsson, 1978).

The preservation and examination of immature stages is discussed exhaustively by Ferrar (1987) and Grodowitz *et al.* (1982).

1.5.4 Illustrations

Line drawings. Line drawings were made with a Leitz-Wetzlar camera lucida mounted on a Leitz-Wetzlar SM-LUX compound microscope.

Scanning electron micrograph (SEM) photographs. Some specimens were critical-point-dried, coated with gold, and photographed through a Cambridge Stereoscan 100 SEM at 25kv accelerating voltage.

1.5.5 Phylogenetics and computer algorithms

Hypotheses of phylogenetic relationships in this thesis were constructed using the methods of Hennig (1966). I am a firm believer in constructing cladograms "by hand", that is without the use of a computer phylogeny program such as PAUP (developed by

D. Swafford, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL, 61820, USA), PHYLIP (Felsenstein, 1989), or Hennig-86 (Farris, 1989). Constructing cladograms by hand forces one to think profoundly about character states and their polarity, rather than simply dumping them in a computer program and accepting the results. It is important, however, to manipulate data, to check for alternate trees that are equally parsimonious, to deal with large numbers of characters, and to take into account homoplasy, all of which can be done much more accurately with a computer. After the phylogenies in this work were constructed, the data upon which they were based were analyzed with the fast and effective program Hennig-86, to check for equally parsimonious conclusions. The exact algorithm suggested by Platnick (1989) as the best in obtaining all most parsimonious trees, "ie*", was used in all analyses.

1.5.6 Categories, ranking, and classification

All taxonomic categories in this thesis refer to monophyletic groups, although the monophyly of some genera may have not been demonstrated adequately yet. Principles of classification, discussed extensively by Wiley (1981), have been followed here. I have tried to adopt a conservative approach to ranking, and have proposed formal groups (genera, tribes and subfamilies) only when these constituted well supported assemblages. Some genera were proposed for taxa with no obvious relationships to any pre-existing taxon, but that had autapotypic character states (for instance *Synaptophora*, *Godavaria* and *Latiborophaga*). There are suggestions (Wiley, 1981) but no rules for proposing formal groups; one is expected to balance the need to show relationships (by grouping taxa) with the needs to show differences (by proposing new taxa) and to preserve well-known, accepted groupings (by minimizing changes). Arguments could be made, for instance, to include all Ironomyiidae, Sciadoceridae and Phoridae in a single family; such a taxon would be as valid as the three currently recognized families, but violates the need to preserve well-known groupings. As a general rule, I did not change the rank of any existing taxa unless there was new evidence that such groupings were not monophyletic.

Classifications using sequencing and subordination, as proposed by Wiley (1981) were used in this thesis. These conventions help to avoid the proposal of countless category ranks for adelphotaxa, when such are not of interest.

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2. OUTGROUPS AND SOME GROUNDPATTERN CHARACTER STATES OF PHORIDAE (DIPTERA)

2.1 Introduction

The closest relatives to the family Phoridae are believed by most dipterists to be the families Ironomyiidae and Sciadoceridae. The relationships among the extant members of these three families, as well as those of the Cretaceous fossil sciadocerids (McAlpine & Martin, 1966), and ironomyiid (McAlpine, 1973), however, have not been resolved satisfactorily. Recent attempts have been made to associate the Cretaceous sciadocerids with extant Sciadoceridae (Disney, 1985; Grimaldi, 1989), or to place them in the Phoridae (Hennig, 1973). Also, an attempt has been made to link Ironomyiidae and Sciadoceridae in a separate monophyletic group (Disney, 1988).

In this paper I describe the terminalia of the newly recollected South American *Archiphora patagonica* (Schmitz) and the Australian *Sciadocera rufomaculata* White (both Sciadoceridae), and examine the relationships among the Ironomyiidae, Sciadoceridae and Phoridae, using the method of phylogenetic systematics (Hennig, 1966). This allows the Ironomyiidae, Sciadoceridae and fossil phorids to be used correctly as outgroups for decisons about character polarity within the Phoridae. To outline the history of this group, I examine the views of McAlpine and Martin, Disney, and Grimaldi before giving my interpretation.

2.2 Material and Methods

Specimens were examined from the following collections, through the cooperation of their curators. Each collection name is preceded by a coden which is used as an abbreviation to refer to material from that collection.

BVB -	collection of the author
CNC -	Canadian National Collection, Biosystematics Research Centre, Agriculture Canada Central Experimental Farm, Ottawa, Ontario, Canada K1A 0C6 (J.M. Cumming)
HO -	collection of Hugh Oliver, Plant Protection Group, Ruakura Agricultural Station, Hamilton, New Zealand

Phylogenetic relationships were determined manually, without computer algorithms, but data sets were analyzed using the program Hennig-86 (Farris, 1989) to check for equally parsimonious results.

2.3 Terms

The dispute over terms used for the male genitalia of cyclorrhaphous Diptera continues unresolved. The epandrial theory (e.g. McAlpine, 1981) and the periandrial theory (Griffiths, 1972) are the two rival ideas that have surfaced; both have their ardent supporters. Some Europeans, especially workers on Orthogenya (Empidoidea), use the terms of Griffiths, while most North Americans use the terms of McAlpine, possibly more because of tradition or convenience rather than disagreement with Griffiths' ideas. As before, I use the terms of the epandrial theory; the equivalent terms of the periandrial theory are listed in Brown (1987).

The terms "synapotypic", "apotypic", "plesiotypic" etc. have been used in this paper as more general terms, rather than "synapomorphic", "apomorphic", "plesiomorphic" and so on that refer only to structure. It seems nonsensical to refer to behavioral or life history characters as -"morphies", even if Hennig (1966) did define holo**morphology** to include physiological and behavioral characters. No behavioral or life history characters were used in this analysis, but the more general term was used as a matter of personal preference. Although using -"typies" seems to me a reasonable convention (as proposed by Tuomikowski, 1967), some people seem to be uncomfortable with this use (e.g. Schuh, 1989). The definition of "apotypic" in Lincoln *et al.* (1982) clearly is not the same as the one used by myself or some others (such as those cited by Schuh, 1989). Other terms not used by Hennig, but subsequently proposed by Ax (1987) are used in this work: adelphotaxon (=sister-group) and groundpattern (=groundplan). The reasons for preferring the use of these more recent terms are those of Ax (1987).

2.4 Description of Taxa

2.4.1 IRONOMYIIDAE

One specimen of *Ironomyia nigromaculata* White was examined. This species was described thoroughly by McAlpine (1967).

Material examined. 1♂, AUSTRALIA: New South Wales, near Gosford, Mooney Mooney Creek, 25.xi.1975, D.K. McAlpine (CNC).

2.4.2 SCIADOCERIDAE

2.4.2.1 ***Sciadocera rufomaculata* White**

Internal characters and terminalia.

Male. Four large, unpigmented rectal papillae present. Malpighian tubules with three openings, four tubules (i.e. one tubule bifurcated basally), two long with swollen ends, two shorter, as in *Megaselia rufipes* (Meigen) (Phoridae) in Schmitz (1916). Testes dark brown. Vasa deferentia enlarged proximally, with thickened, gland-invested walls; joined as common sperm duct only in epandrium; entering aedeagus between forks of arm and exiting through basal ring. Right side of abdomen with dorsolateral, crescent-shaped sclerite. Epandrium asymmetrical, left side larger. Left side of epandrium (Fig. 2.1A) deep, bare; left surstylus round, with dorsal, digitiform projection. Right side of epandrium shallow, bare; broad, sclerotized process (right surstylus or dorsal bridge?) extended from right hypandrial arm to left surstylus. Hypandrium without processes. Aedeagus (Fig. 2.1C) tube-like, but differentiated into basal ring (basiphallus?) and distal furcation; with small dorsal sclerite. Attachment of aedeagal guide anterior to ring, tip of furcation attached to right side of hypandrium.

Female. Four large rectal papillae. Two long spermathecae. Two round, multilobate accessory glands. Tergite and sternite 7 well developed, almost continuous laterally. Tergite 10 not divided, but with loss of pigmentation at the mid-point; tergite 10 also deflected downward at mid-point.

Remarks. The configuration of the aedeagus makes it impossible to swivel it forward. It seems to be mounted backwards compared to the aedeagus in Phoridae.

Disney (1986) shows a division of tergite 10, that is absent from specimens I examined. Instead, the tergite is deflected ventrally at the midpoint.

Material examined. AUSTRALIA: New South Wales [no other datal] (BVB; about 100 specimens in alcohol, some of which were dissected and discarded); NEW ZEALAND: Hamilton, Claudelands Bush Reserve, 1♂, 1♀; 9-10.ix.1970, 2♂, 15.iii.1972, H.A. Oliver (HO); 1♂, T.O., Pareora State Forest, Toa Toa bush, 3.iii.1984, H.A. Oliver (HO).

2.4.2.2 *Archiphora patagonica* (Schmitz)

Sciadocera (*Archiphora*) *patagonica* Schmitz 1929

Archiphora patagonica (Schmitz), Hennig 1964

The existence of only a single male and female specimen of *Archiphora patagonica* did not encourage potentially damaging dissections. In 1988, however, Dr. Lubomir Masner of the Biosystematics Research Centre in Ottawa, Canada, collected extensively in southern Chile, recapturing virtually all of the taxa described by Schmitz (1929, 1931). I obtained several specimens of *A. patagonica* from his Malaise trap, pan trap and sweep samples. This species was described capably by Schmitz (1929), but the details of the male and female terminalia were not included in this description. Since these structures are of great importance in phylogenetic studies, the internal characters and male and female terminalia of *A. patagonica* are described below.

Male. Testes brown, small. Vasa deferentia do not form common sperm duct. Crescent-shaped sclerite of unknown homology present between abdominal tergite 6 and terminalia. Epandrium asymmetrical, left side larger. Left side of epandrium deep (Fig. 2.1B), setulose; left surstylus free, with medially pointed, darkly sclerotized process. Right side of epandrium shallow, with few setulae; right surstylus attached to epandrium by thin membrane, elongate, darkly sclerotized. Hypandrium without processes, setulose. Aedeagus (Fig. 2.1D) short tube, with some vague areas of sclerotization. Basiphallus and apical sclerites not differentiated. Hypoproct setulose.

Female. Ovipositor divided into two sections: proximal section smooth, cylindrical, with apical pores; apical section (Fig. 2.1E-F) slightly curved, almost completely encased in membrane with dense concentration of barbed spinuli (Fig. 2.1E), apically pointed.

Material examined. CHILE. 1♂, 2♀, Chiloe, 70m, Ahori Alto, primary forest, 23.ii.1988, L.Masner, sweep; 1♀, Llanquihue, El Chingue, nr. Correntoso, 18.ii.1988, L.Masner, 200m, sweep, *Nothofagus*; 4♂, Malleco, 3 km W. Victoria, 250m, 26.ii.1988, L.Masner, screen sweep; 1♂, 1♀, Osorno, Puyehue National Park, 13.ii.1988, L.Masner, *Nothofagus*, 2♂, 3♀, Puyehue National Park, Anticura, 12-14.ii.1988, L.Masner, *Nothofagus* forest; 1♀, Valdivia, 500m, 30 km W. La Union, Las Trancas, *Nothofagus*, 7-12.ii.1988, L.Masner, sweep (BVB, CNC).

Remarks. The specimens of this species are small and were slightly decomposed, so that observation of the internal organs was very difficult in male specimens and impossible in female specimens.

The wing venation, as illustrated by Schmitz (1929) and reproduced by McAlpine and Martin (1966) is different from that found in my specimens (Fig. 2.2). In my specimens the venation is much more similar to that of *Sciadocera*, with the basal portion of M_1, as well as the common stalk of M_1 and M_2, reduced to a faintly visible fold (Fig. 2.2).

The female terminalia of this species are highly specialized, possibly for laying eggs in a plant or animal host.

2.4.3 PHORIDAE

2.4.3.1 *Prioriphora* McAlpine and Martin 1966

The holotypes of all four described species in this genus were examined (Brown & Pike, 1990).

2.4.3.2 *Sciadophora* McAlpine and Martin 1966

I examined the holotype specimen of *Sciadophora bostoni* from the private collection of Mr. P. Boston. This is the only described species in this genus.

My illustration of the wing of this species (Fig. 2.1G) differs significantly from that given by McAlpine and Martin (1966). The anterior wing margin is more convex, the costa is shorter, and the base of vein M fades out basally. I could not make out details of vein Sc.

2.5 History of the Classification of the Phoridea

The Phoridea comprise a monophyletic group within the Cyclorrhapha. There has been some dispute over the proper rank, and therefore the correct name of the group that includes the Phoridae and related families; Latreille (1829) first used the name Hypocera, Coquillett (1901) first used the name Phoroidea to refer to the

Lonchopteridae + Phoridae, and Hennig (1948) first used the name Phoridea to refer to a group including the Platypezidae, Sciadoceridae, and Phoridae. In his discussion of the major subordinate groups of the Cyclorrhapha, Griffiths (1972) tentatively considered the Platypezidae not to be more closely related to the Phoridae than to the rest of the Cyclorrhapha, thus breaking up a group including the Platypezidae, Sciadoceridae, Ironomyiidae and Phoridae (the Phoroidea of McAlpine & Martin, 1966). He used the name Hypocera (=Phoridea) for the families Ironomyiidae, Sciadoceridae and Phoridae, but that name is also the name of a phorid genus (*Hypocera* Lioy), as pointed out by Disney (1988). The name Phoridea is now preferred by Griffiths (personal communication), as its ending implies the same rank as his Platypezidea and Syrphidea, but Disney (1988) uses Phoroidea for this group. Griffiths (1972) accepted McAlpine and Martin's (1966) concept of families within the Phoridea, excluding the Platypezidae.

Hennig (1976) pointed out that the partially reversible circumversion of the male hypopygium in Platypezidae, as well as several other characters, were probably plesiotypic with respect to the rest of the Cyclorrhapha, foreshadowing the recent view that the Platypezidae are the sister-group to the rest of the Cyclorrhapha (Griffiths, personal communication).

The Phoridea is based mainly on the character wing vein Sc fused to R_1 (McAlpine & Martin, 1966). In Ironomyiidae, only the middle portion of Sc is fused to R_1 (Figs. 2.1H-I), but the apex of Sc is lost or fused with R_1 in all other Phoridea (Fig. 2.2 for example). Two species have been described in Ironomyiidae, the extant *Ironomyia* *nigromaculata* and the Cretaceous fossil *Cretonomyia pristina* McAlpine (1973). The only tentative synapomorphy for these two genera is antennal pedicel with a finger-like projection. The other synapomorphy proposed by McAlpine (1973), Sc partially fused to R_1 (Fig. 2.1H-I), is a primitive state with respect to the rest of the Phoridea and cannot be used to justify the family Ironomyiidae itself. The degree of fusion of vein Sc to R_1 is much greater in *Ironomyia* than *Cretonomyia*, such that if the antennal synapotypy is not accepted, the Ironomyiidae could be considered a paraphyletic group relative to the rest of the Phoridea. If this is shown to be so, the two species either would have to be considered single types of monobasic families Cretonomyiidae and Ironomyiidae, or would have to be treated as the most basal lineages of an expanded Phoridae.

The Sciadoceridae consists of two extant species, *Sciadocera rufomaculata* White (Australia, New Zealand) and *Archiphora patagonica* (Schmitz) (south Chile). Three further species have been assigned to this group, namely the Canadian Cretaceous amber fossils *Sciadophora bostoni* McAlpine and Martin and *Prioriphora canadambra* McAlpine and Martin, and the Eocene/ Oligocene Baltic amber fossil *Archiphora robusta* (Meunier). Hennig (1964) placed *Napomyza robusta* (Agromyzidae) Meunier in *Archiphora*, recognizing that it belonged to the Sciadoceridae, and at the same time elevated the subgenus *Archiphora* to full generic status.

Schmitz (1929) argued that the earlier suggestion of Tonnoir (1926) to include the Sciadoceridae as a primitive subfamily of the Phoridae was wrong because Sciadoceridae had many similarities with Platypezidae. These similarities are known now to be in retained primitive character states (Hennig, 1964). Since these character states were unknown in any described phorid, Schmitz dismissed the idea that Sciadoceridae belonged in the Phoridae, based on the prevailing idea that overall resemblance was the best measure of relatedness, an idea now superseded by relatedness based on synapotypy (Hennig, 1966). Schmitz recognized one genus and two subgenera of Sciadoceridae, *Sciadocera s.s.* and *S.* (*Archiphora*).

2.6 The Views of McAlpine And Martin (1966) and McAlpine (1989)

McAlpine and Martin made a first attempt to show the relationships of the families of the Phoridea. In describing the two Cretaceous fossil taxa *Prioriphora* and *Sciadophora*, they constructed a hypothesis of relationships among these families. From the synapotypies in the character matrix of McAlpine and Martin (Fig. 2.3), however, it can be seen that the relationships they proposed were not all based on synapotypy, especially in the lineage giving rise to extant sciadocerids, which is based solely on symplesiotypy. Analysis of this data set (re-coded in Table 2.1a) using Hennig-86 gave two most parsimonious cladograms, collapsible into a single consensus tree (Figs. 2.4A-C). These trees show that almost none of the branching patterns suggested by McAlpine and Martin (1966) (Fig. 2.4D) were supported by this character matrix. Therefore, no convincing evidence, in the form of synapotypies, had yet been put forward to link *Sciadocera* and *Archiphora*.

Also, the group they called Sciadoceridae is a paraphyletic assemblage, as was first pointed out by Hennig (1973). By excluding the Phoridae from the family Sciadoceridae, they constructed a group that did not contain all of the descendants of a common ancestor. Paraphyletic groups are accepted in some instances where there is a perceived historical, evolutionarily demonstrable or sentimental value to the taxon (as in the grade group Reptilia), but especially in such a small group of inadequately known flies, the recognition of this paraphyletic group is unacceptable. Hennig (1973) removed the Cretaceous fossil genera *Prioriphora* and *Sciadophora* from the Sciadoceridae and re-classified them in the Phoridae.

Recently, McAlpine (1989) has defended the idea that the Aschiza is a monophyletic group and the sister taxon to the Schizophora. Within the Aschiza he recognizes two groups: the Syrphoidea (Syrphidae and Pipunculidae) and the Platypezoidea. The classification within the Platypezoidea is (sequentially) Platypezidae, Lonchopteridae, Ironomyiidae, Sciadoceridae and Phoridae. Many of the characters that support this phylogeny, however, are questionable, as follows:

1) The character state "pupal respiratory horns enlarged" is used to justify the Aschiza, in spite of the fact that these horns are absent from Platypezidae. Evidence suggests that the character state "hypopygium incompletely rotated" used by Hennig and Griffiths (but ignored by McAlpine) should be used to classify the Platypezidae separately from the rest of the Cyclorrhapha.

2) The clade of Sciadoceridae + Phoridae is supported by the character state "C ending

at R_{4+5}", yet this state is also found in Ironomyiidae, as shown by McAlpine (1967, 1973) and in Lonchopteridae (Peterson, 1987a). The thickening of the hind margin of the wing in Lonchopteridae is interpreted as secondary by McAlpine himself (1989, pg. 1422).

3) "Cell dm reduced" cannot be used to justify the Sciadoceridae, as this state is found also in *Prioriphora*. It should be noted that McAlpine still considers *Sciadophora* and *Prioriphora* to be Sciadoceridae (pg. 1424) although previously (McAlpine & Martin, 1966) claiming that these taxa lacked the synapotypy given here by McAlpine (cell dm reduced).

4) In the text (pg. 1423-1424), McAlpine gives the character "... form of the antennal pedicel is unique (Hennig, 1976)" to further justify the Sciadoceridae, but this structure appears to me to represent only an intermediate stage between a larger pedicel in Platypezidae and the greatly reduced pedicel in Phoridae.

5) In the text (pg. 1424), McAlpine states that the loss of sclerotized spermathecae may be an apotypy of Phoridae, however these also are lacking from Sciadoceridae.

2.7 The Views of Disney (1985, 1988)

Disney is not convinced of the hypothesized relationships between the families within the Phoridea. Based on an aberrant cross vein in the wing of a heavily parasitized specimen of *Megaselia pleuralis* (Wood) (Phoridae) (Disney, 1985), it was hypothesized that the nomenclature of the thin wing veins in the Phoridae was wrong. Disney proposed that the cross vein between M_1 and M_2 represents vein dm-cu, so that the two longitudinal veins it joined would have to be M_{1+2} and CuA_1. He proposed that fusion of $M_1 + M_2$ was synapotypic for the Phoridae, but absent from the two Cretaceous fossils *Sciadophora bostoni* and *Prioriphora canadambra*, which he removed to the Sciadoceridae.

The argument that the cross-vein in the aberrant *Megaselia pleuralis* specimen is a recapitulation of the medial cross-vein in more primitive Diptera (such as Platypezidae) can be made only with recourse to taxa related most closely to the Phoridae (Ironomyiidae and Sciadoceridae). Instead, Disney compared this aberrant specimen to a dolichopodid, a member of the distantly related Orthogenya. The wing veins of closely related Ironomyiidae, particularly those of *Cretonomyia* (Fig. 2.1I), have the fork of M_1 and M_2 cross-vein-like, that appears to be a much better candidate to homologize with the aberrant cross-vein. Thus, if there has been any recapitulation, probably it would have been toward a M_1 - M_2 cross vein, rather than toward the cross vein between M_2 and CuA_1.

A larger question remains, however, about the admissibility of such evidence. I hold that the data from a single, heavily parasitized fly, such as the specimen of *Megaselia pleuralis*, are highly suspect. Similar cross veins have been found in other Diptera (Glasgow, 1960; Hawley & Georghiou, 1970; Thompson, 1974), often produced by abnormal conditions during development, such as low temperature. The authors of the glossinid and drosophilid works believed that some of these veins may have phylogenetic significance, but this can be shown only through proper outgroup comparison. As I have shown above, the outgroup evidence from the Ironomyiidae points towards a M_1 - M_2 cross vein.

Other anomalous wing veins are known in the Phoridae. For example, Gotô and Takeno (Fig. 3b, 1983) reported a small fork at the tip of wing vein CuA_1, while Oliver (personal communication) notes a similar fork near the tip of vein M_1. Again, these are similar to the many short wing vein spurs in *Drosophila* and *Glossina*, most of them produced by various abnormal environmental conditions. Given a large enough sample, such forks probably could be found on all of the thin wing veins, and are unlikely to represent any phylogenetic recapitulation.

Therefore, like Hennig (1973), I do not support the separation of *Sciadophora* and *Prioriphora* from the rest of the Phoridae or their placement in a paraphyletic Sciadoceridae.

Disney (1988) has proposed that *Sciadocera*, *Archiphora* and *Ironomyia* have a pattern of costal setae differing from all other Diptera examined by Hackman and Väisänen (1985). He proposed that this new type of pattern (B4, following the terms of Hackman and Väisänen) is a synapotypy for the group Sciadoceridae + Ironomyiidae, separating them from other members of the Aschiza (a group that many except McAlpine (1989) believe is paraphyletic).

To examine the plausibility of these proposals, the states found in other, related groups must be examined. Hackman and Väisänen reported type B1 pattern to be widespread: "setae in two, seldom three, longitudinal rows, each row with homomorphous setae... hairs or bristles" (Hackman & Väisänen, 1985, pg 171). Disney's B4 is characterized as "two rows of homomorphous spinulae". The difference between Disney's "spinulae" and Hackman and Väisänen's "bristles" is seen to be a semantic one, when Disney's (1988) illustration is compared to Hackman and Väisänen's Fig. 14. Here, the "bristles" in the costa of the platypezid *Callomyia amoena* Meigen show a striking similarity in size and shape to those illustrated by Disney for *Sciadocera*. Comparison with other Platypezidae in my collection shows that many of the "bristles" that are characteristic of type B1 are much closer to the "spinulae" in Fig. 1 of Hackman and Väisänen, and that some Platypezidae (e.g. *Paraplatypezina* sp.) even have relatively shorter and thicker setae. Since Hackman and Väisänen contend that the condition shown in the Platypezidea, which is the putative primitive outgroup to the Phoridea, and most Orthogenya is type B1, this is probably the primitive state. Therefore, I reject Disney's proposed synapotypy for the Sciadoceridae + Ironomyiidae versus the rest of the Aschiza. Instead, I agree with McAlpine and Martin (1966) and others that the wing vein Sc fused to R_1 is a valid synapotypy for the Phoridea.

2.8 The Views of Grimaldi (1989)

In a paper describing some phorid fossils, Grimaldi (1989) proposed that

Prioriphora canadambra belonged in the Phoridae, while *Sciadophora bostoni* should be placed in the Sciadoceridae. His reason for excluding *Sciadophora* from the Phoridae is that the wing "venation is plesiomorphic with respect to phorid venation at the family level" (pg.69). In the absence of new character states to link *Sciadophora* with other sciadocerids, however, the grouping of these two taxa is based on symplesiotypy. This procedure establishes again a paraphyletic Sciadoceridae, like that of McAlpine & Martin (1966) before Hennig's emendation.

Grimaldi lists the following characters as primitive for *Sciadophora*: veins C and R_{4+5} reach nearly to apex of wing; stem and fork of M_1 and M_2 retained; vein M_{3+4} (here referred to as CuA_1 using the terms of the Manual of Nearctic Diptera) originating at distinctive bm cell. Similarly he lists the following characters as derived for *Prioriphora canadambra*: thickened, dark radial veins, that are shortened like the costal vein; veins M_1, M_2, and M_3 (the last presumably referring to M_{3+4} or CuA_1) unbranched and nearly parallel. Most of these differences disappear, however, when the original specimens are examined, and the inaccuracies of the illustrations are exposed. In *Prioriphora* the costa is actually longer than shown (misinterpreted because the wing is bent), and the thickness of the radial veins is exaggerated. In *Sciadophora* the wing is much closer to that of *Prioriphora* than the illustration in McAlpine and Martin (1966) indicates (compare with my figure), such that the costal vein is shorter, and the medial veins are actually subparallel. In fact, the argument for the retention of a separate genus *Sciadophora* relative to *Prioriphora* is weak, based only on the longer body setae and the relatively complete stem of veins M_1 and M_2.

Observation of wing veins in amber is problematic, however, as discussed below (Apotypy 11).

Therefore, I do not accept the placement of *Sciadophora* in the Sciadoceridae, as suggested by Grimaldi.

2.9 Reconstructed phylogeny of the Phoridea

Hypothesized Synapotypic Character States.

I have identified useful (synapotypic) character states from among those proposed by McAlpine and Martin (1966) as justification for the groups they established, added a few new synapotypic states, and presented them in a strictly cladistic framework (Fig. 2.5).

1a Wing vein Sc fused to R_1 at mid-length (Fig. 3, McAlpine, 1967; Fig. 10, McAlpine, 1973).

b Wing vein Sc fused to R_1 on apical two-thirds, including apex (Figs. 18- 22, McAlpine & Martin, 1966).

2 Antennal pedicel with finger-like projection (Figs. 1,2, McAlpine, 1967; Figs. 6,7, McAlpine, 1973).

3 Fork of wing veins M_1 and M_2 shifted basally (Figs. 18-21, McAlpine & Martin, 1966).

4 Wing cross-vein dm-cu shifted basally (Figs. 18-21, McAlpine & Martin, 1966).

5 Stigma lost (Figs. 18-21, McAlpine & Martin, 1966).

6 Radial veins of wing thickened (Figs: 18-20, McAlpine & Martin, 1966).

7 Male frons widened (Figs. 4,12, McAlpine & Martin, 1966).

8a Anal lobe of wing reduced (Figs. 17-22, McAlpine & Martin, 1966).

b Anal lobe of wing markedly reduced (Fig. 18, McAlpine & Martin, 1966)

This character (8b) is the justification given by Hennig (1964) for the genus *Archiphora*. It is notable that the venation of the two species, the extant *A. patagonica* and the fossil *A. robusta*, is identical, except for the base of the medial veins (see character 11).

9 Only one sclerite between segment 6 and male terminalia.

10 Ejaculatory apodeme lost.

11 Basal section of wing vein M_1, and stem of M_1 plus M_2 faint or absent.

As noted above, the wing illustration given by Schmitz (1929) and copied by McAlpine and Martin (1966) for *Archiphora patagonica* differs from my specimens. Illustrations of *Archiphora robusta* (Hennig, 1964) have the basal segment of this vein present, representing either a phylogenetic reversal, extrapolation of a structure not actually seen by Hennig (although Hennig states that in *A. robusta* the stem of the medial vein is well developed), or distortion because of amber preservation (see below). Re-examination of *Prioriphora canadambra*, as well as three new species of *Prioriphora* (Brown & Pike, 1990) indicates that a faint or absent medial base is widespread. In *Sciadophora*, only the base of veins M_1 and M_2 is reduced, representing either a reversal, a retained primitive state, or inability to correctly discern this structure (see below). This state was coded as being equivocal for *Sciadophora* (Table 1b).

Observation of wing veins in amber-preserved fossils is problematic. As can be seen in Fig. 2.2, the base of the medial veins is still slightly visible in the extant *Archiphora patagonica*, and such visibility is apparently enhanced when viewing wings at an angle. Therefore, the venation of fossil specimens can be seen accurately only when a wing is parallel to the surface of the amber, a relatively rare occurrence. In a piece of amber containing *ca* 30 specimens of *Prioriphora intermedia* Brown and Pike, specimens at an angle to the field of view often apparently had the base of the medial veins present, but specimens parallel to the field of view clearly showed the medial bases reduced.

12 Flagellomere 1 enlarged in male (e.g. Fig. 2a, Schmitz, 1929)

This is the only defensible synapotypy of the family Sciadoceridae at this time. The first flagellomere of *Prioriphora intermedia* is also somewhat enlarged, however, and this character state is also widespread in Phoridae. Thus, the cladistic justification of Sciadoceridae is weak.

13 Empodia absent (McAlpine, 1989).

Unfortunately, I was unable to see this character in the fossil Phoridae.

14 Vasa deferentia do not form common sperm duct.

In one species of Lonchopteridae, the putative outgroup of the Phoridea (McAlpine, 1989), the two vasa deferentia fuse after coming together in a seminal vesicle. In one species of Platypezidae (species examined was *Plesioclythia agarici* (Willard)) the vasa deferentia retain their identity (do not share a common lumen), but are fused along most of their length. In extant Phoridae, the two ducts are fused and have a common lumen along most of their length, as in Lonchopteridae. In *Sciadocera* and *Archiphora*, these ducts are unfused along their entire length. Unfortunately, this character state cannot be observed in the fossil specimens, and may be part of the ground pattern of the Phoroidea. The state of this character in Ironomyiidae also needs to be examined.

15 Wing vein CuA_2 lost or reduced, wing cell cu*p* lost (Figs. 20-22, McAlpine &

Martin, 1966).

This cell absent from all fossil species examined, but vein CuA_2 is faintly present in some phorids (for example Peterson, 1987b, Fig. 47,53).

16 Base of M_1 and M_2 shifted forward, appearing to arise from R_s (Figs. 20- 22, McAlpine & Martin, 1966).

17 Proscutellum lost.

This state was given by McAlpine and Martin (1966), but its usefulness is questionable, as I am unable to verify it in *Prioriphora canadambra* or to see it in the other species of *Prioriphora*.

Although somewhat tenuously supported, I maintain that the phylogeny of the Phoridea, as proposed by McAlpine and Martin (1966) and emended by Hennig (1973), is the best explanation of the evolutionary patterns found in these insects. Based on the synapotypies given above (coded in Table 1b), a cladogram was constructed that is identical to that of McAlpine and Martin. Subsequent analysis with Hennig-86 showed that this is the single most parsimonious cladogram. The weakest point in the phylogenetic hypothesis is the support for the family Sciadoceridae, which in the future may be found not to be a monophyletic group. Inclusion of *Sciadocera* and *Archiphora* in an expanded concept of the Phoridae would then be called for.

Evolution of character states in the Phoridea

The direction of evolution in the Phoridea has been mostly towards reductions: wing veins shorten and disappear, femoral setae are lost, and tergites between abdominal segment 6 and the terminalia in males are reduced and lost. The reduction of wing veins probably is associated with the reduction of body size in Phoridae, as these reductions occur in other small insects (O'Hara, 1988). This pattern has led to some skepticism about the value of these character states in the present classification system (Disney, 1981); however, no convincing alternatives have been advanced.

The male terminalia are among the most important structures for determining relationships between phorid genera, and deserve special mention. The male terminalia of fossil specimens are obscured by their preservation in amber, but the character states found in extant sciadocerids and ironomyiid demonstrate the following ground pattern character states for Phoroidea:

1) Terminalia asymmetrical.
2) Surstyli on both sides separate, not fused to epandrium.
3) Aedeagus simple, tube-shaped.
4) Hypandrium without prominent processes and with short setulae only. These two character states are more variable in Lonchopteridae and Platypezidae.

The ground pattern structure of the female terminalia of Phoridea can be inferred only from *Sciadocera rufomaculata*, because female specimens of *Ironomyia nigromaculata*, *Archiphora patagonica* and *Sciadophora bostoni* all have derived, possibly parasitic-type ovipositors. Reference to female Lonchopteridae and Platypezidae, more distantly related, putative outgroups for the Phoridea, are also useful.

1) Tergite 7 present in female. Tergite 8 is absent from *Sciadocera* and primitive phorids, and may represent another synapotypy of the Phoridea.

2) Tergite 10, or 9 + 10, present, in *Sciadocera* with anterior, ventrally deflected process. As Disney (1986) hypothesized, the anterior process is probably the precursor of the U-shaped sclerite between tergite 8 and tergite 10 in most female phorids.

3) Internal sclerotized loop of female reproductive system absent. This loop, found in females of many genera of Phoridae, was considered by Disney (1986) to be homologous with sternite 9 in Asiloidea. Its absence from Platypezidae, Lonchopteridae, Ironomyiidae, and Sciadoceridae, however, shows that this character state is neomorphic within the Phoridae.

Other character states belonging to the ground pattern of the Phoridea, and that are relevant to classification within the Phoridae, are listed below. The presence of these character states in Phoridae is plesiotypic.

1) Palpus one-segmented. This state is present in *Sciadocera*, *Archiphora*, Platypezidae and Lonchopteridae.

2) Anepisternum undivided.

3) Four rectal papillae present.

4) Tibiae with setae present, without longitudinal setal combs.

5) Malpighian tubules of *Megaselia rufipes* - type (see Schmitz, 1916).

2.11 Significance of fossils in the phylogeny of the Phoridea

As Hennig (1966) and others have shown, many fossils are of little help in performing phylogenetic reconstruction. Although they are undeniably interesting, fossils of Phoroidea have contributed little to the classification of this group that could not have been deduced from extant taxa. Ax (1987) has pointed out three types of information available from fossils, after they have been classified, that are here applied to the situation in the Phoridea:

1) The geological age of closed descent communities. The family Phoridae, and therefore its adelphotaxon the Sciadoceridae, as well as the Ironomyiidae (McAlpine, 1973), are already known to have been present in the Cretaceous period.

2) The sequence of evolution of constitutive features of a taxon. This information is

summarized in the cladogram of relationships (Fig. 2.4).

3) A contribution to deciding between plesiotypy and apotypy. Little has been gained in this regard, because many of the phylogenetically useful character states are either not visible (for example male terminalia, presence of proscutellum, condition of the sperm ducts) or absent (supra-antennal setae) from the fossil taxa, or differ little from states found in the Sciadoceridae.

2.12 Acknowledgements. I am grateful to Hugh Oliver for sending me numerous specimens of *Sciadocera rufomaculata*, Philip Boston for loan of the holotype specimen of *Sciadophora bostoni*, J.M. Cumming for the loan of Platypezidae and *Prioriphora canadambra*, G.C.D. Griffiths for information on phylogeny of the Phoridea and C. Sabrosky for information on nomenclature. G.E. Ball is gratefully acknowledged for commenting on earlier versions of this paper, and D.C. Currie and E.R. Fuller gave valuable opinions on a number of matters. This research was partially funded by a Natural Sciences and Engineering Research Council grant to G.E. Ball, and an NSERC postgraduate scholarship to the author.

Table 2.1. Distribution of plesiotypic and synapotypic character states among Ironomyiidae, Sciadoceridae and Phoridae. 1 - synapotypic, 0 - plesiotypic, ? - state unknown or equivocal.

a) Character states from McAlpine and Martin (1966).

Taxa	
Sciadophora	11111110000000000000
Prioriphora	001110111111100001110
A. robusta	0000110111111000000000
A. patagonica	000011111110010000001
Sciadocera	000001111100111110000

b) Character states from this paper's analysis.

Characters	12345678901234567
Taxa	
Ironomyiidae	1100000000000?000
Sciadocera	20111111111111000
Archiphora	20111112111111000
Sciadophora	2011111111?0??110
Prioriphora	201111111110??111
Phoridae	20111111111100111

Figs. 2.1A-I. Character states of adult Ironomyiidae, Sciadoceridae, and Phoridae (scale bar = 0.1mm). Figs. B-D to same scale, Figs. E-F to same scale, no scale given in originals of Figs. H-I. A, Epandrium of *Sciadocera rufomaculata* White, left lateral; B, epandrium of *Archiphora patagonica* (Schmitz), left lateral; C, aedeagus of *Sciadocera rufomaculata* White, left lateral (anterior to right); D, aedeagus of *Archiphora patagonica* (Schmitz), left lateral; E, apex of ovipositor of *Archiphora patagonica* (Schmitz), dorsal, bracket indicates extent of barbed spinuli (only a small number actually shown); F, apex of ovipositor of *Archiphora patagonica* (Schmitz), spinulose membrane removed, lateral; G, wing of *Sciadophora bostoni* McAlpine and Martin; H, wing of *Ironomyia nigromaculata* White, arrow indicates crossvein of significance (see text), modified from %%355%%, used with permission. I, wing of *Cretonomyia pristina* McAlpine, arrow indicates crossvein of significance (see text), modified from %%510%%, used with permission. Abbreviations: a - apex of ovipositor, b - basal ring, s - surstylus.

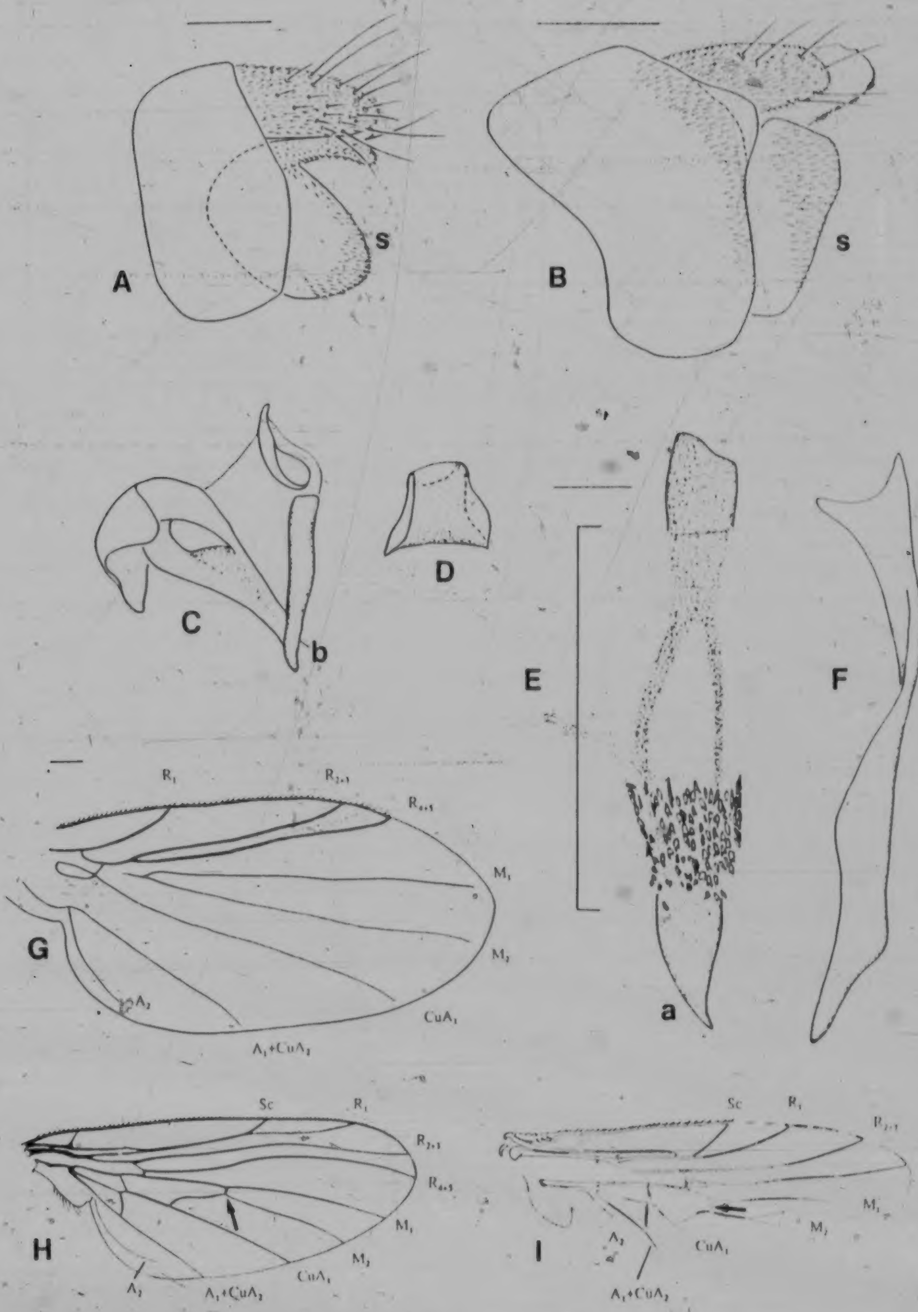

A
s
B
s
C
b
D
E
a
F
G
R_1
R_{2+3}
R_{4+5}
M_1
M_2
A_2
CuA_1
A_1+CuA_2
H
Sc
R_1
R_{2+3}
R_{4+5}
M_1
M_2
CuA_1
A_2
A_1+CuA_2
I
Sc
R_1
R_{2+3}
R_{4+5}
M_1
M_2
A_2
CuA_1
A_1+CuA_2

Fig. 2.2. Wing of *Archiphora patagonica* (Schmitz).

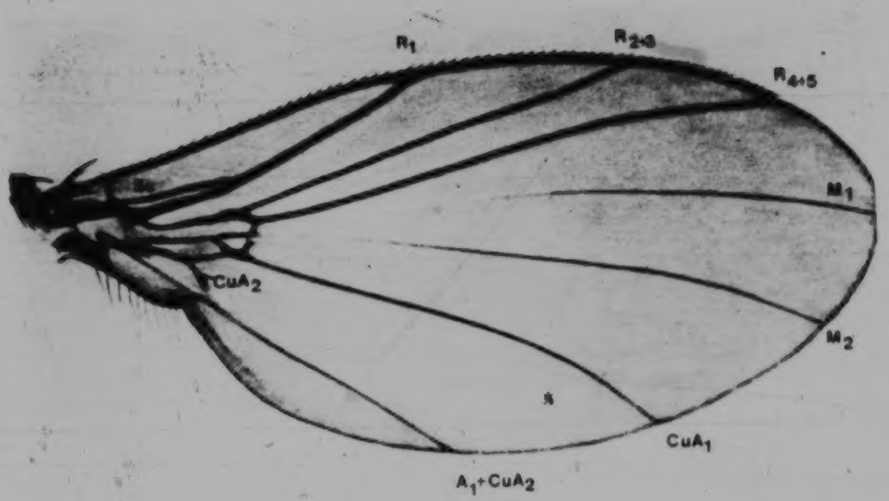

R$_1$
R$_{2+3}$
R$_{4+5}$
M$_1$
CuA$_2$
M$_2$
CuA$_1$
A$_1$+CuA$_2$

Fig. 2.3. Representation of hypothesized synapotypic character states presented by McAlpine and Martin (1966), plotted on their preferred cladogram.

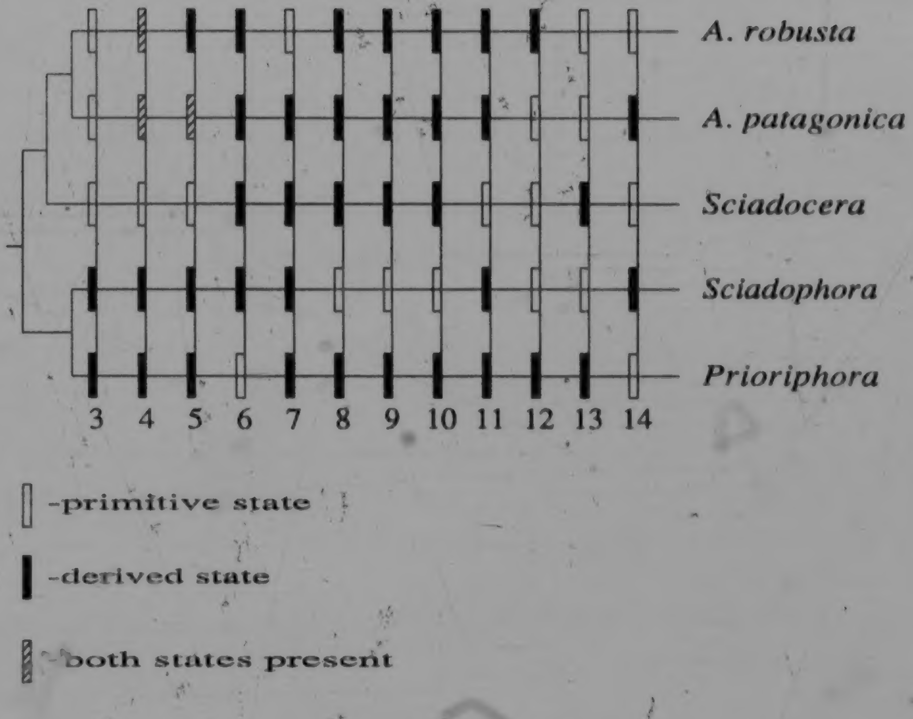

A. robusta
A. patagonica
Sciadocera
Sciadophora
Prioriphora
-primitive state
-derived state
-both states present

Fig. 2.4. Cladograms of the relationships of the Sciadoceridae of McAlpine and Martin (1966). A-B, two most parsimonious cladograms from their data; C, concensus cladogram from their data; D, their published cladogram.

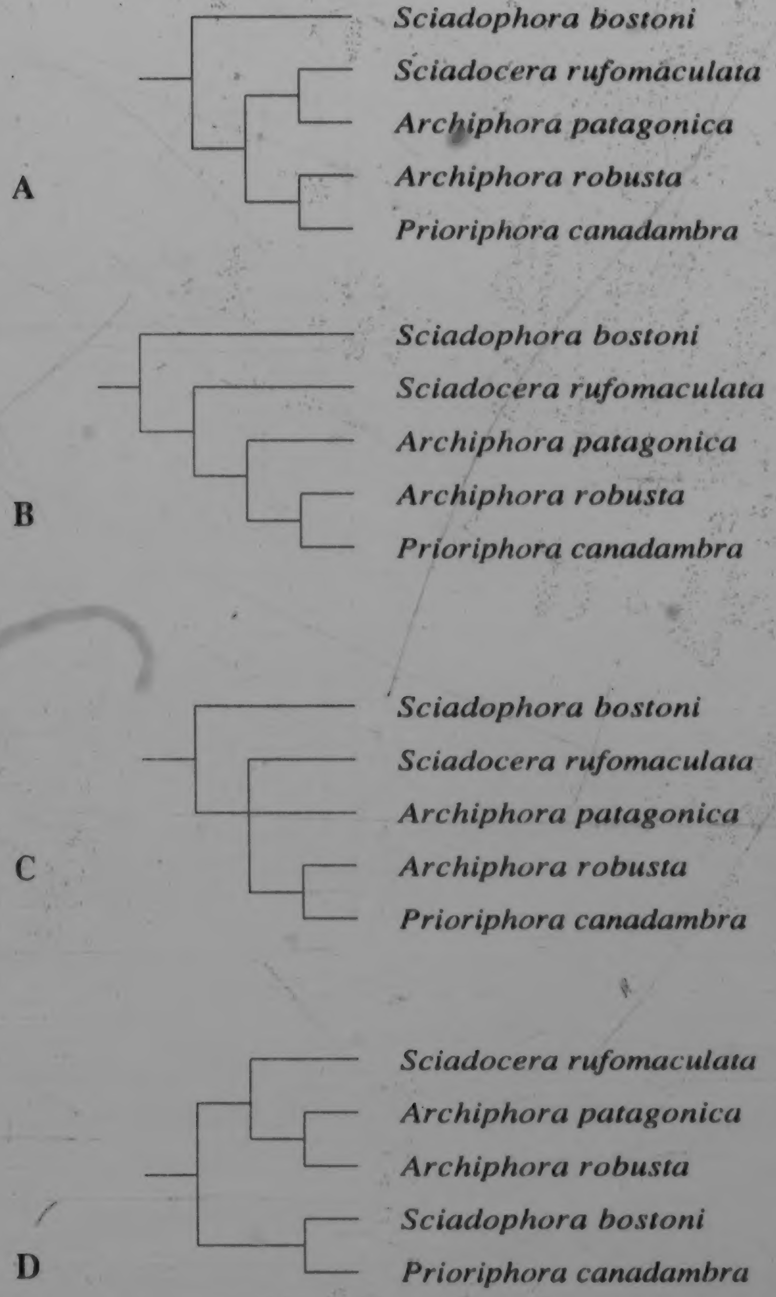
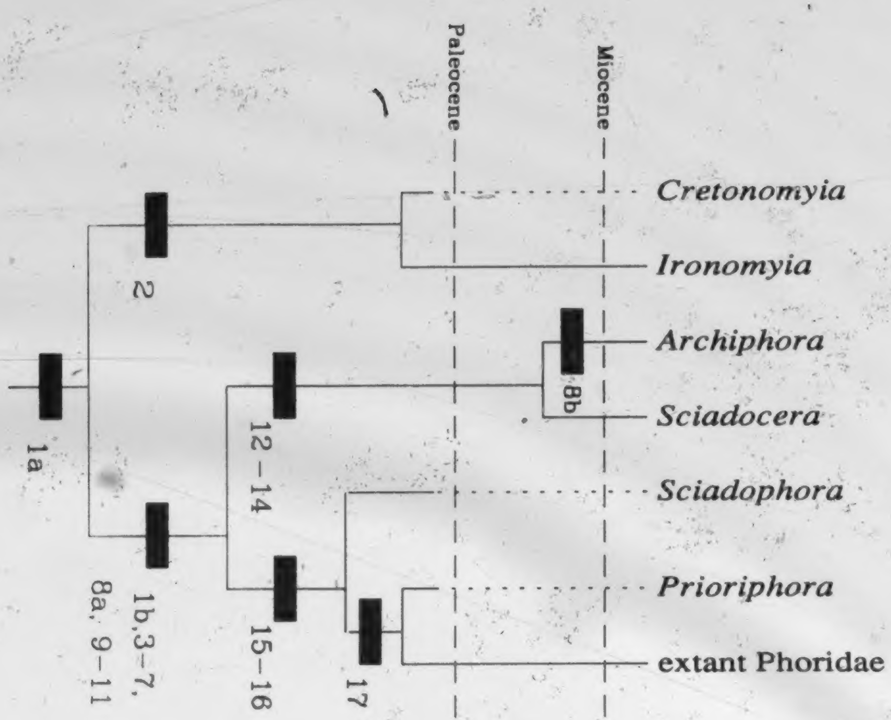

A
Sciadophora bostoni
Sciadocera rufomaculata
Archiphora patagonica
Archiphora robusta
Prioriphora canadambra
B
Sciadophora bostoni
Sciadocera rufomaculata
Archiphora patagonica
Archiphora robusta
Prioriphora canadambra
C
Sciadophora bostoni
Sciadocera rufomaculata
Archiphora patagonica
Archiphora robusta
Prioriphora canadambra
D
Sciadocera rufomaculata
Archiphora patagonica
Archiphora robusta
Sciadophora bostoni
Prioriphora canadambra

Fig. 2.5. Cladogram depicting relationships of the Phoridea, as recognized in this paper.


Paleocene
Miocene
Cretonomyia
Ironomyia
Archiphora
Sciadocera
Sciadophora
Prioriphora
extant Phoridae
1a
2
1b,3-7,
8a, 9-11
12 -14
15-16
17
8b

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3. GROUNDPATTERN CHARACTER STATES AND SUBFAMILY CLASSIFICATION OF PHORIDAE (DIPTERA) OF THE NEARCTIC REGION

3.1 Introduction

Previous classifications of the Phoridae have been based on phenetic and phylogenetic groupings. The two major subgroups of the Phoridae are the Phorinae and Metopininae, of which the Metopininae was considered probably monophyletic and the Phorinae was considered to be possibly paraphyletic by Hennig (1973). No synapotypic characters have been proposed for the Phorinae, which has been defined traditionally by the presence of tibial setae, reclinate supra-antennal setae and an undivided anepisternum (e.g. Borgmeier, 1964). All of these character states are primitive with respect to the Metopininae.

Similarly, the relationships of a third, highly divergent, subfamily, the Aenigmatiinae, are uncertain. While many of the species of this group (see Brown, submitted) probably form a monophyletic assemblage, they show no obvious relationship to either of the other subfamilies.

Three other subfamilies of Phoridae are recognized: the Alamirinae, Termitoxeniinae, and Thaumatoxeninae. All species of these groups are found in the Old World tropics, and are not considered further in this revision.

In this paper I discuss the phorid groundpattern (Ax, 1987) and propose a hypothesis for the phylogeny and re-classification of the phorids of the Nearctic Region formerly placed in the subfamilies Phorinae and Aenigmatiinae. Monophyletic groups are proposed based on synapotypic characters (Hennig, 1966) found in Nearctic taxa and primitive phorids from other world regions. Their placement in the new classification is discussed also.

3.2 Materials and methods

Most of the material used in this revision is from the collection of the author and will be listed in detail in future publications about the phylogeny of the various subgroups. The type specimen of *Synaptophora critica*, gen.n., spec.n., was borrowed from the Canadian National Collection (abbreviated as CNC), Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, Canada, K1A 0C6 (J.M. Cumming).

Taxa from outside of the Nearctic Region were used frequently for comparison and to test hypotheses based on Nearctic specimens. Because of our limited knowledge about the Neotropical, Oriental, Australasian and Afrotropical phorid faunas, many of the species from these regions were not identified to species. This is in recognition of the incomplete coverage given by existing keys, as well as the realization that there are a great many undescribed species in regions outside of North America and Europe.

Full taxonomic synonymies are not given in this paper, except for those not found in Borgmeier (1968, 1971).

Male terminalia were examined by treatment in hot 10% KOH, and rinses of 30% acetic acid, water, and alcohol. Then, they were placed in an evaporating dish with a drop of glycerine and about 2ml of alcohol, and were put on a warming tray to allow the alcohol to evaporate. Next, terminalia were placed in glycerine jelly on glass slides and examined with light microscopy.

Some specimens were gold-coated and examined with a Cambridge 100 Scanning Electron Microscope.

Hypothesized relationships were reconstructed using standard cladistic techniques (Hennig, 1966). The cladogram in this paper was constructed manually, without computer algorithms. The data set was checked subsequently with the computer program Hennig-86 (Farris, 1989) to seek additional equally parsimonious cladograms.

Any phylogenetic analysis must have a logical starting point, provided by an outgroup (Watrous & Wheeler, 1981). As expressed previously (Chapter 2), I regard the outgroup for extant Phoridae to be species of Ironomyiidae and Sciadoceridae, as well as the relatively primitive Cretaceous fossil phorids *Sciadophora bostoni* McAlpine and Martin and *Prioriphora* species (Brown & Pike, 1990; McAlpine & Martin, 1966). Other, more distant outgroup taxa are Lonchopteridae, Platypezidae, and Opetiidae.

Although both Dr. R.H.L. Disney and I espouse phylogenetic methods (Hennig, 1966), we come to different conclusions about the true phorid outgroup. I accept the Sciadoceridae, Ironomyiidae, Platypezidae and Orthogenya (Empidoidea) as sequential outgroups for the Phoridae, while Disney apparently does not. Furthermore, there are some philosophical differences in our approaches. Disney (1988) regards the development of a neomorphic structure several times to be less likely than the presence of this structure in the groundpattern (common ancestor) of the group and its subsequent loss in several places. While I would agree with this principle, there are other possible explanations for spotty character occurrence. One is the concept of underlying synapomorphy (Saether, 1979; Sluys, 1989; Tuomikowski, 1967), which is defined as "agreement in capacity to develop parallel similarity" (Tuomikowski, 1967; pg 141). Thus, there may be an underlying genetic potential to express these structure [illegible] sion may not be as unlikely as evolving the structure *de novo*. The existence of underlying synapotypies seems to be widespread in the Phoridae, with characters such as longitudinal tibial setal combs, medial frontal furrow and elongate, pointed antennal flagellomeres occurring in many groups. Under these conditions, one must examine the immediate outgroup to the Phoridae for assignment of character polarity within the family, instead of searching the lower Diptera as Disney (e.g. 1988) has done. Thus, while the Tabanidae and the Mycetophilidae have fully developed median frontal furrows, such are absent from taxa of the outgroups of the Phoridae. Their appearance in some phorid genera may be considered an underlying synapotypy, rather than a groundpattern character state.

A different explanation for spotty character state distributions is discussed by Cooper (1990), who postulates that many primitive character states "disappear long before their genetic mechanisms pass beyond the capacity for reexpression." These primitive character states, which he calls atavisms, are present in relatively derived taxa not as neomorphic states, but rather as re-expressed primitive states. Therefore, in the preceding example, the frontal furrow would be considered an atavistic character state, re-expressing the ecdysial cleavage line (Snodgrass, 1947; see below) of more primitive Diptera. Regardless of the mechanism by which these character states are expressed, however, outgroup comparison shows clearly that a complete frontal furrow is not part of the phorid groundpattern. Naturally, there are problems in determining the difference between an atavism and a neomorphic character state; for instance, determining how far back in the history of a taxon must one go before one can discount atavisms. Cooper (1990) proposed that the atavistic character states in his study dated from the common ancestor of the genus he was studying and its adelphotaxon. Increasingly distant taxa having the primitive character state make the proposal of atavisms in relatively more derived taxa tenuous, as a greater time of separation makes changes in the underlying genetic structure more likely. A palpus with two segments (see below) is found in some phorids, but absent from most others, as well as from all outgroups. The most closely related taxon with a two-segmented palpus is an empidoid (Chvála, 1983), although it is also present in "most orthorrhaphous Brachycera" (McAlpine, 1981). At least the families Opetiidae, Platypezidae, Lonchopteridae, Ironomyiidae and Sciadoceridae, however, apparently lack this character state. Since these families are part of the Cyclorrhapha, dating at least from the Cretaceous (80 million years ago), the underlying genetic potential to express a two-segmented palpus must have been conserved, but suppressed, for an extremely long period of time. Similarly, toothed tarsal claws are known from one species of phorid (Disney & Kistner, 1989a), although they are present in some nematocerous Diptera. Whether their presence in phorids an atavism, or a neomorphic character is unknown, but since the origin of the Brachycera (a group including Phoridae which is the adelphotaxon of at least some nematocerous group) dates as far back as the Upper Triassic (Hennig, 1981), an atavism would have been suppressed intact for an extraordinarily long period of time before being re-expressed. It is impossible to answer this question without an understanding of the genes themselves, but there is little doubt that the concept of atavisms is an important one.

Another factor to consider when stating what is parsimonious, and what is not, is the pattern of phylogeny within the group. There are many instances that can be imagined when the independent derivation of a new character is far more parsimonious than its inclusion in the groundpattern. An example is the presence of a two-segmented palpus in individuals classified in the genera *Dicranopteron* Schmitz, *Diplonevra* Lioy, *Dohrniphora* Dahl, *Myopiomyia* Disney, *Palpiclavina* Silvestri, one species of *Diocophora* Borgmeier and one species of *Megaselia* Rondani. The first four genera belong to a monophyletic group, while the latter three represent single instances among hundreds, if not thousands, of known species. Therefore, the two segmented palpus, which is absent from all outgroups, need only have arisen four times, rather than being a groundpattern state that subsequently was lost innumerable times in most Phoridae.

3.3 Terms

Recent reviews of Diptera phylogeny have postulated adelphotaxon (Griffiths, 1972), ancestor-descendant (Chvála, 1983) or no special relationship (McAlpine, 1989) between the Orthogenya and Cyclorrhapha. This disagreement affects the terms used to refer to the male genitalia, and I deal with it as I have previously (Brown, 1987b).

The terms synapotypic, apotypic, plesiotypic etc. have been used in this paper as more general terms, rather than synapomorphic, apomorphic, plesiomorphic and so on which refer only to structure (Chapter 2, Terms). Other terms not used by Hennig, but subsequently proposed by Ax (1987) are used in this work: adelphotaxon (=sister-group) and groundpattern (=groundpian). The reasons for preferring the use of these more recent terms are those of Ax (1987).

3.4 Homology of terminalia

Equivalent terms. To clarify the following arguments, I give the equivalent terms for structures used by Disney, Griffiths and me.

Brown	Disney	Griffiths
♂ terminalia		
Epandrium	Epandrium	Periandrium
Hypandrium	Hypandrium	Hypandrium
Ring-shaped sclerite	Segment 10	n/a
♀ terminalia		
Sclerotized loop	furca (sternite 9)	n/a
U-shaped sclerite (tergite 9+10, in part)	tergite 10	tergite 10 (in part)

tergite 9+10 (in part) epiproct tergite 10 (in part)

3.4.1 Homology of male terminalia.

Disney (1986a, b) believes that he has evidence that there is no close relationship between the Orthogenya and Cyclorrhapha. He rejects the periandrial theory of Griffiths (1972, see terms section) for the Cyclorrhapha, instead restricting its validity to the Orthogenya (Eremoneura exclusive of the Cyclorrhapha). Disney believes the older epandrial theory best explains the origin of the male genitalia in Cyclorrhapha, and since most of the evidence for relationship between the Orthogenya and Cyclorrhapha is based on the periandrial theory, that this relationship must be questioned.

Based partly on two new species of *Diplonevra* (*D. mortimeri* and *D. watsoni*) Disney (1986b) argues that the ring-shaped sclerite between the cerci and epandrium of males of the phorid genus *Dohrniphora* and the stalk upon which the cerci are mounted in males of *Diplonevra* are derived from the fusion of tergite and sternite 10. According to Disney, since the sclerites of segment 10 are hypothesized to be absent from the Cyclorrhapha (Griffiths, 1972), their presence in the Phoridae would be a plesiotypic character state relative to the Orthogenya. Furthermore, the dorsal sclerite anterior to "tergite 10" would have to be tergite 9, or the epandrium, which Griffiths hypothesized is lost from Cyclorrhapha. Disney lists two possibilities in the formation of this ring:

i) Tergite 9 (epandrium) lost, periandrium immediately divides transversely to form a new "post-periandrium" which was later lost in most genera, post- periandrium extended ventrally to fuse and form ring.

ii) Ancestral tergite and sternite 10 fuse laterally, large dorsal sclerite anterior to ring is therefore tergite 9.

I believe that a third alternative to the two given by Disney is far more plausible:

iii) Neomorphic "ring" formed on apical tip of periandrium/ epandrium in monophyletic group including *Diplonevra* and *Dohrniphora* only.

There is no need to postulate that the periandrium/ epandrium immediately divided transversely and the "post periandrium" was lost in most phorid genera, especially since all outgroups lack this structure.

3.4.2 Homology of female terminalia.

A further paper by Disney (1986a) contends that tergite and sternite 9 are retained in females of the genus *Chonocephalus* Wandolleck, as is a partially sclerotized, spherical spermatheca. He argues that the Phoridae retain 10 tergites in the adult female and thus the Phoridae (and therefore the Cyclorrhapha) are plesiotypic with respect to the Orthogenya, and can not be derived from them.

i) Disney states that since three sclerotized spermathecae are present in Platypezidae and Syrphidae, they were probably a groundpattern condition for the Phoridae as well. Most phorids have elongate, unsclerotized spermathecae, but in *Chonocephalus* there is a single, sclerotized, spherical spermatheca which Disney interprets as primitive.

Disney ignores postulated sister-group relationships between the Phoridae, Sciadoceridae and Ironomyiidae, and the availability of the more primitive phorids (such as Hypocerinae, Aenigmatiinae, Phorinae, Conicerinae, and *Triphleba*) as a functional outgroup. Disney argues that three spherical, sclerotized spermathecae are primitive, yet they are lacking from females of *Sciadocera* and all North American phorid genera (except *Chonocephalus*) which have small, elongate, unsclerotized spermathecae. Furthermore, the spermathecae are remarkably posterior in the body. This indicates that the spermathecae in *Chonocephalus* are neomorphic, not plesiomorphic.

ii) The argument is made by Disney that sternite 9 is present in the groundpattern of the Phoridae, based on the presence of a sclerotized loop in the wall of the reproductive tract of *Chonocephalus*, which Disney believes is homologous with the furca found in Asilidae. A similar loop is found also in *Gymnophora* (Brown, 1987b), *Rhopica* Schmitz (Gotô, 1985b), *Beckerina* Malloch, some *Megaselia* (Benner & Curtis, 1988), *Hypocera americana* Borgmeier, *Thalloptera schwarzmaieri* Borgmeier, at least one species of *Diplonevra* and species of many other genera. Again, the loop is absent from Platypezidae, Ironomyiidae, and Sciadoceridae, and thus cannot be homologized with the furca of lower Diptera unless one wishes to hypothesize a plethora of independent losses. While the tissue forming this ring undoubtedly originates from the area forming sternite 9 in more primitive Diptera, I dispute that it is directly homologous with the furca. Instead, I believe that it is a neomorphic structure, possibly part of the phorid groundpattern, or is a sporadically expressed underlying synapotypy.

iii) Finally, Disney (1986a) hypothesizes that the U-shaped sclerite on the female ovipositor is a retained tergite 10, followed by a more posterior epiproct. According to McAlpine (1981), there is no true epiproct (tergite 11) in female Diptera, but the fused structure formed by tergites 9 and 10 is often referred to by this name. In female *Sciadocera*, there is a large posterior plate (tergite 9+10) that is bent at mid-length. This structure is not divided (as reported by Disney, 1986a) in specimens that I observed, nor did my specimens have the forward-pointed, U-shaped arms figured by Disney (1986a, Fig. 3b).

I believe that the anterior, U-shaped sclerite found in Phoridae is homologous to the anterior portion of the tergite 9+10 in *Sciadocera* which has separated from its parent sclerite (tergite 9+10), and thus represents a neomorphic structure. The form of these sclerites in *Chonocephalus* is a modified version of this groundpattern. Evidence for this interpretation is given by examination of the character states throughout the family. Females of Hypocerinae, such as *Hypocera ehrmanni* Borgmeier, Phorinae, such as *Chaetopleurophora eurythronota* (Strobl) (figured in Disney, 1986a), *Anevrina*

Lioy and *Phora*, and Aenigmatiinae such as *Diplonevra* and *Dohrniphora*, have tergite 9+10 similar to that of female *Sciadocera*, with a small terminal section and a larger, anterior portion, which may or may not be separate. Females of *Triphleba laticosta* Borgmeier have a similar arrangement, but the anterior margin of the anterior portion (which is not separated from the posterior portion) has two arms extending into the previous segment. Such arms are also visible in female specimens of *Anevrina spinipes* (Coquillett), and some other *Triphleba* species, although they are shorter. In females of *Beckerina* and other metopinines (such as *Megaselia* Rondani), the final stage of development is evident, with the anterior portion separate and two long, thin arms present (see Disney, 1986a, Fig. 4c, T10).

Therefore, Disney's (1986a) assumption that the abdomen of *Megaselia* is primitive, since it has the largest number or sclerites, is shown to be incorrect by outgroup comparison with *Sciadocera* and other, relatively more primitive phorids. The groundpattern condition for Phoridae is tergite 7 absent, tergite 8 absent (see below), and tergite 9+10 not forming a U-shaped sclerite. Disney's contention that the phorid groundpattern is more primitive than that of Orthogenya is not supported.

3.5 Groundpattern states of certain characters in the Phoridae

3.5.1 *Head*

1) Supra-antennal setae reclinate (Fig. 3.1A).

No discernible supra-antennal setae are present in Platypezidae, Lonchopteridae, Ironomyiidae, Sciadoceridae, and *Prioriphora*. Thus, the outgroup evidence is equivocal as to whether dorsally pointing (reclinate) supra-antennal setae are part of the groundpattern. Ingroup evidence, however, shows that individuals of the relatively primitive Phoridae with large tibial setae (Phorinae in the traditional sense) have reclinate supra-antennal setae, as do members of the relatively primitive metopinine genus *Triphleba* Rondani. In the single known specimen of *Sciadophora*, there are three pairs of small, upward pointing, interfrontal setae that may represent the two pairs of anterior interfrontal and one pair of supra-antennal setae in other Phoridae, but this is purely speculative. If however, these setae are the homologues of the supra-antennal setae, then they provide further support for this character. Disney's (1988) assertion that the frontal setation of *Megaselia*, with downward pointing (proclinate) supra-antennal setae (Fig. 3.1B), is close to the phorid ground plan is unfounded in the absence of outgroup evidence.

2) Median furrow rudiment present (Figs. 3.2A-F, 3.3A-D).

Based on outgroup comparison, an anterior rudiment of the median furrow is part of the phorid groundpattern. This structure is a shallow indentation in the lower portion of the frons, in at least one instance with a small pore at the bottom (Fig. 3.2B, p). A rudimental furrow is found in various phorid groups (Figs. 3.2A-D), whereas a complete median furrow is found in adults of *Coniceromyia* Borgmeier and

Phora Latreille (both Phorinae), perhaps *Conicera* Meigen (Conicerinae) (but see Figs. 3.2E-F), and many, but not all Metopininae. Outgroup taxa, including various female specimens of Platypezidae, such as *Agathomyia* Verrall (Figs. 3.3A-B), *Platypeza* Meigen, and *Polyporivora* Kessel & Maggioncalda, show anterior traces of this furrow (as noted by Disney, 1988), as do *Lonchoptera* Meigen (Fig. 3.3D) and female *Ironomyia* White (according to McAlpine, 1967). The "vestigial median furrow" in the original illustration of *Archiphora patagonica* Schmitz (Disney, 1983), was described by Schmitz (1929a) as part of a "large depressed groove along the middle line (which practically takes up one-third of the breadth of the frons)". The anterior rudiment of the furrow, however, is also distinct. The furrow is apparently absent from individuals of *Sciadocera* (Fig. 3.3C), and the Cretaceous fossil phorid genera *Sciadophora* and *Prioriphora* (Brown & Pike, 1990; McAlpine & Martin, 1966), although the preservation of the fossils may preclude its observation. Thus, the outgroup evidence for a complete furrow being primitive in all of the Phoridae (as proposed by Disney, 1988) is lacking.

Disney (1988) argues that a complete median furrow is present in the groundpattern of the Phoridae. This structure, he believes, is homologous with the "broad, ill-defined trough" found in a platypezid (*Plesioclythia argyrogyna*) and the epicranial suture (= coronal or metopic suture, Snodgrass, 1935) in various other relatively more primitive Diptera, such as Tabanidae and Mycetophilidae (Peterson,A, 1916). Snodgrass (1947) reviewed the epicranial suture, found mostly in larval insects, and proposed the new name "ecdysial cleavage line of the head", since it is not a true suture. He came to the further conclusion that:

> "The so-called "epicranial suture", with its coronal stem and frontal arms, is, in the immature insect, a preformed line of weakness in the head cuticle along which the cuticle will split at ecdysis. The cleavage line may be carried over into the adult, though usually it is more or less suppressed or entirely absent in the imago; other grooves in the adult cranium have frequently been mistaken for it, and designated the "epicranial suture" (Snodgrass, 1947).

Direct homology of a complete median furrow with the ecdysial cleavage line of the head is unlikely when the taxa bearing each character state are so distantly related. The median furrow could be an atavistic character state (Cooper, 1990), but outgroup evidence tends to refute this hypothesis. Therefore, I regard a complete furrow as neomorphic.

Disney's statement (1988) that it is more parsimonious to have this structure as part of the phorid groundpattern, then reduced and lost several times in the Phoridae, rather than it being neomorphic, is without basis. Since Disney offers no phylogenetic hypothesis (cladogram) upon which to plot these character states and count steps, there is no way to test which is the most parsimonious transformation. Proper use of the available outgroup, as outlined above, however, shows the true polarity of this character state.

3) Palpus one-segmented.

A two-segmented palpus is found in *Dohrniphora*, *Diplonevra* (Schmitz, 1938), *Myopiomyia* (Disney, 1987), *Dicranopteron* (Disney, 1990a), *Palpiclavina* (Disney & Kistner, 1989b), *Diocophora appretiata* Schmitz (Disney & Kistner, 1989a) and *Megaselia biarticulata* Disney (1988). The first four genera probably form a monophyletic group, while *Palpiclavina*, *Diocophora appreciata* and *M. biarticulata* are far removed from these genera. Based on these occurrences, plus the fact that a two-segmented palpus occurs in "most orthorrhaphous Brachycera" (McAlpine, 1981), Disney (1988) postulates that it belongs to the phorid groundpattern.

Examination of the phorid outgroup shows that the two-segmented palpus is absent from adults of Lonchopteridae, Platypezidae, *Sciadocera* and *Archiphora* Schmitz (Sciadoceridae). It is present in adult individuals of the Hybotidae (Empidoidea), but was regarded by Chvála (1983) as an autapotypy for the family, not part of any groundpattern. Thus, there is little evidence for a two-segmented palpus being part of the phorid groundpattern.

Disney's (1988) argument that it is more parsimonious to consider the two-segmented palpus a plesiotypic character state, instead of a neomorphic trait or an atavism as discussed above, so far has little support. Loss of this structure in several lineages involves far more evolutionary steps than its independent acquisition in a few individual species.

4) Arista dorsal.

The arista is located apically on flagellomere 1 in Platypezidae and Ironomyiidae, but is dorsal in female Sciadoceridae, *Sciadophora* and *Prioriphora*.

3.5.2 *Thorax*

1) Anepisternum without dorsoventral furrow (=anepisternum undivided) (Fig. 3.1C, a).

The most important character found on the thorax is the presence of a divided anepisternum (Fig. 3.1D, af), used by Schmitz (1929b) to distinguish the subfamily Metopininae Rondani, in an emended sense. Disney (1983) suggested that:

> "When supposedly absent (Fig. 10), it is possible that some of the elements of this furrow are present but close to the edges of the mesopleuron."

His "Fig. 10" showed the pleural region of *Conicera dauci* (Meigen), with the anepisternum undivided, but with a suggestive looking suture on the posterodorsal corner. This posterodorsal fold, however, is found also in many phorids with the usual, dorsally curved suture. Thus, if this represents the "elements" of the furrow Disney refers to, they are not homologous with the true anepisternal suture.

2) Anepisternum bare.

In *Ironomyia*, there are numerous, thin hair-like setae on the anepisternum, but in most Lonchopteridae, Platypezidae, Sciadoceridae, and *Prioriphora*, the anepisternum is bare. Two exceptions are *Cretonomyia* (Ironomyiidae), with several short setulae and *Sciadophora*, with one large posteriorly directed and three medium sized, anterodorsally directed setae. McAlpine and Martin (1966) considered a bare anepisternum to be a derived character for the Phoroidea, but the outgroup evidence is unclear, with the Platypezidae indicating a bare anepisternum is primitive, and the Ironomyiidae possibly indicating that a setulose anepisternum is primitive. The alternating outgroup method of Maddison *et al.* (1984) is not helpful in this instance, as the first (*Prioriphora*) and last (Ironomyiidae) outgroup within the Phoridea have different character states. I consider tentatively the character state anepisternum bare to be primitive (based on *Prioriphora*), but a setulose anepisternum arises in several lineages.

3) Dorsum of thorax without single median row of acrostical setae.

As discussed by Hennig (1976), outgroup comparison indicates the true polarity of this character state within the Phoridea. Individuals of *Opetia nigra* Meigen (Opetiidae) have undifferentiated thoracic chaetotaxy (Kessel & Maggioncalda, 1968) as do *Ironomyia*, but all Platypezidae, Sciadoceridae, *Sciadophora*, and *Prioriphora* have the single row of acrostichal setae with a row of dorsocentral setae on each side. Adults of *Lonchoptera* (Lonchopteridae) have both rows of dorsocentral setae, but lack the unpaired acrostical row.

In the extant Phoridae, I am unaware of any genera with individuals bearing an acrostichal or dorsocentral seta row. Most have an evenly setulose scutum, but females of *Spiniphora* Malloch have an extra pair of dorsocentral setae which likely are derived secondarily.

3.5.3 *Wing*

1) Vein R_{2+3} present.

This vein is present in all outgroups, including the Cretaceous amber fossils.

2) Vein Sc fused to R_1.

Disney (1981) objected to this character as a groundpattern feature of the Phoridae, on the grounds that individuals of certain genera (*Conicera* was his example) have the tip of Sc free. This is doubtlessly a secondarily derived state, however, as the series of *Cretonomyia*, *Ironomyia* to *Sciadocera* shows a clear transformation, with Sc fusing at mid-length to R_1 in the single known specimen of *Cretonomyia* McAlpine (Ironomyiidae), the reduction of the apical portion of Sc adult *Ironomyia* and later the loss of apical portion in adults of *Sciadocera* and the rest of the Phoroidea.

3.5.4 *Legs*

1) Large, unpaired setae present on tibiae.

Tibial setae are present on the tibia of individuals in outgroup taxa such as Sciadoceridae and the Cretaceous phorids.

2) Hind tibia without dorsal, longitudinal rows of enlarged setulae.

In adults of Ironomyiidae, Sciadoceridae and Cretaceous phorids there are no rows of enlarged setulae on the hind tibia. Furthermore, the genus *Burmophora* Beyer and several other relatively primitive hypocerine genera (see below) that lack these setal rows, can be shown to be the relatively plesiotypic adelphotaxa of the relatively more derived genera such as *Borophaga* Enderlein, which have a pair of setal rows. This indicates that within the Hypocerinae, a pair of setal rows has evolved independently. Other groups also have evolved these structures independently.

Disney, however, (1988, 1990b) has proposed that one or more of these setal combs (Fig. 3.3E, e) are part of the phorid groundpattern, citing their widespread distribution and their presence in one species of Platypezidae. In light of their absence from the phorid outgroup, however, their presence in some platypezids and the phylogenetically distant Mycetophilidae (Disney, 1988) cannot be used as evidence of their primitive state.

Disney (1990b) also claims that outgroup comparison shows that the groundpattern of Phoridae includes two rows of enlarged setulae on the mid tibia. This claim can be shown to be suspect when the evidence is examined: Disney's evidence consists of a single species of platypezid. Even if all Platypezidae, however, had two setal rows on the mid tibia, these structures are absent from the legs of Ironomyiidae and Sciadoceridae, the undoubted adelphotaxa of Phoridae. Using parsimony and the outgroup method of comparison (Maddison *et al.*, 1984) the absence of setal rows is obviously the groundpattern character state in the Phoridae and no convincing case can be made for them being primitive.

3.5.5 *Abdomen*

1) Epandrium and hypandrium anteriorly fused (Figs. 3.4A-B).

This character state is discussed below.

2) Hypandrium without basal, hypandrial, setae.

The subfamily Metopininae is justified partially by the presence of a pair of setae at the base of the aedeagal apodeme (Fig. 3.1E) as in adult males of *Gymnophora* Macquart (Brown, 1987b, figs. 50-51). This character state will be discussed further below.

3) Testes white.

The testes of male specimens of *Sciadocera*, *Archiphora* and Platypezidae are brown in color.

4) Female tergite 7 absent.

Adult females of most Hypocerinae, Phorinae, Aenigmatiinae, Conicerinae, *Rhopica* (not Nearctic; see below) and *Triphleba* lack this structure, although it is present in female *Sciadocera*. The absence of this structure is apparently a groundpattern apotypy of the family Phoridae.

5) Female tergite 8 absent.

Adult females of *Sciadocera*, Phorinae, Aenigmatiinae, *Conicera*, *Rhopica* and *Triphleba* lack this structure. Its absence is clearly part of the phorid groundpattern.

3.5.6 *Adult gut*

1) Rectal papillae not in a separate pouch.

Some Phoridae, namely *Diplonevra* and *Dohrniphora*, have the rectal papillae in a separate pouch, not in the main gut tract. This character state is also found in *Sciadocera rufomaculata*, but not *Lonchoptera* sp., *Plesioclythia agarici* (Willard) and *Agathomyia* sp. (both Platypezidae). Therefore, the outgroup evidence for the Phoroidea (Sciadoceridae + Phoridae) shows that rectal papillae in a separate pouch is a derived character state in *Sciadocera*. Within the Phoridae, this state is absent from *Anevrina olympiae* (Aldrich), *Borophaga subsultans* (Linnaeus), *Epicnemis* Borgmeier sp., *Megaselia rufipes* (Meigen), *Multinevra* Disney (undescribed species), *Phora* sp., *Spiniphora excisa* (Becker), *S. spinulosa* (Malloch), and *Triphleba lugubris* (Meigen). It is far more parsimonious to derive this character state twice, once in *Sciadocera*, once in *Diplonevra* and *Dohrniphora*, than to postulate it is part of the phorid groundpattern and derive it once (in Sciadoceridae + Phoridae), but lose it five or more times (from Hypocerinae, Phorinae, Aenigmatiinae other than *Diplonevra* and *Dohrniphora*, Conicerinae, and Metopininae).

2) Four Malpighian tubules, with three openings; two long with swollen ends, two shorter.

The basic number of these structures in Diptera is four (Hennig, 1973), but in Phoridae there are apparently 2-4 (Schmitz, 1916) in different configurations. This character was studied by Schmitz (1916), who described several groups based on number and form of these structures, as follows:

A) 2 openings, 2 tubules,
ends swollen - some *Megaselia*, *Gymnophora*

B) 3 openings, 3 tubules - i) short, anterior two somewhat swollen - subfamily Termitoxeniinae (not Nearctic)
ii) long, with simple ends - *Spiniphora*

C) 3 openings, 4 tubules - i) 2 long, with swollen ends, 2 shorter - *Megaselia rufipes*

ii) all long, with simple ends - *Chaetopleurophora*

In this classification, openings refer to the number of tubule stems that actually articulate with the rest of the gut, regardless of distal furcations. For instance, *Megaselia rufipes* has three main trunks opening into the gut, but one of these is distally furcated.

Other taxa were examined as follows:

Taxon	Type of Arrangement
Megaselia araneivora (from Gotô, 1985a)	C i
Sciadocera rufomaculata	C i
Triphleba lugubris	either B or C
Contopteryx illustris	C (either i or ii)
Spiniphora bergenstammi	B ii
Physoptera membranosa	A (possibly; at least two tubules, both with swollen ends)
Apocephalus paraponerae	Ci

Note that, based on outgroup comparison, type Ci as found in *Sciadocera* is the primitive state. More taxa need to be examined before any phylogenetic conclusions can be drawn.

3.6 Reconstructed phylogeny of the Phoridae

A phylogeny (Fig. 3.5) and new classification is proposed for the subfamilies of Nearctic Region Phoridae. Five subfamilies are recognized: Hypocerinae, Phorinae, Aenigmatiinae, Conicerinae and Metopininae. The relationships among the relatively primitive subfamilies are proposed tentatively, as they are based on the fusion of the surstyli to the epandrium, a series of character states that may have been subject to some homoplasy; nevertheless, they support a single most parsimonious cladogram (determined using Hennig-86). The outgroups for this analysis were the families Sciadoceridae and Ironomyiidae.

The genus *Rhopica*, known from the Bismark Archipelago and Papua New Guinea, but not found in the Nearctic Region, was included in this analysis to indicate some important character states. Similarly, the genera *Triphleba* and *Beckerina* Malloch were highlighted in this revision which is concerned otherwise with higher taxa.

3.6.1 *Hypothesized synapotypic character states* (see also Table 3.1)

1 Venational distinctions of phorids.

The distinct wing venation of extant Phoridae serves as an adequate synapotypy to group all known species separately from other members of the Phoridea.

2 Left surstylus fused to epandrium.

In outgroup taxa and *Burmophora*, both surstyli are separate from the epandrium. This character state serves as the main justification to group the hypocerines as the adelphotaxon of the rest of the Phoridae, and to link the Aenigmatiinae, with the Conicerinae and the Metopininae. Within these groups, however, the character states are various and not always the same as the groundpattern conditions. For example, except for the relatively most primitive genus *Burmophora*, male hypocerines all either lack surstyli, or else they are imperceptible after fusing with the epandrium. Further deviations from the groundpattern occur, for instance in the male of *Megaselia biarticulata* Disney (1988), which has a secondarily separate left surstylus.

3 Right surstylus fused to epandrium.

4 Epandrium and hypandrium broadly fused anteriorly (Figs. 3.4A-B).

This character state, as well as #5 and #10 belongs to a group of traits that are absent from some relatively more derived, monophyletic sub-groups of the taxa they define.

The fusion of epandrium and hypandrium is found in males of Hypocerinae, Aenigmatiinae, Phorinae, Conicerinae, and the metopinine genera *Rhopica* and *Triphleba*, but is absent from the outgroup, *Beckerina*, and most other Metopininae.

The most parsimonious interpretation (verified with Hennig-86) of such a character state distribution is that the fused condition was present as a newly evolved trait in the common ancestor of all phorids, but was later lost or reversed in the lineage including *Beckerina* and most other Metopininae. The interpretation of this character state as a synapotypy to link the Hypocerinae, Aenigmatiinae, Phorinae, Conicerinae, *Rhopica* and *Triphleba* must be rejected, based on characters #6, which links *Triphleba* with other Metopininae, and #8, which links *Rhopica* with other Metopininae, exclusive of *Triphleba*.

5 Tergite 7 absent

The same arguments given for synapotypy #4 apply for this character state.

6 Hypandrial setae present (Fig. 3.1E).

The presence of these setae has been noted by many workers, but apparently their significance has been overlooked. The basal hypandrial setae are found in males of many genera of Metopininae, and also in those of the genus *Triphleba*, previously considered part of the primitive subfamily (former Phorinae) of phorids. Their presence in *Triphleba* males indicates that this genus either must be transferred to a more inclusive Metopininae, or that a new subfamily, Triphlebinae, should be proposed as the adelphotaxon of the Metopininae. I prefer to include *Triphleba* in the

Metopininae, as a further proliferation of subfamily names is undesirable, and because some species of *Triphleba* have a faint anepisternal furrow, a character linking the undoubted Metopininae.

7 U-shaped sclerite present.

As discussed above, tergite 9+10 (so-called epiproct) of the female abdomen is composed of an anterior and posterior portion that are either fused or separate in the phorid groundpattern. In females of relatively derived taxa, such as *Megaselia* and most other metopinines, the anterior portion is distinctly separate, and forms a U-shaped sclerite with thin, anteriorly directed arms. Forward directed arms are also found in the anterior portion of the tergites in females of some relatively primitive genera (*Anevrina*, *Triphleba*), but these do not seem to be directly homologous with those found in Metopininae.

8 Anepisternal furrow present (also referred to as anepisternum divided) (Fig. 3.1D).

This character state has been considered for a long time the defining trait of the Metopininae, yet some taxa with an anepisternal furrow were referred to the relatively primitive former subfamily Phorinae because they had large tibial setae. Since large tibial setae are present in the phorid outgroup (Sciadoceridae), however, their occurrence is a primitive character state, which cannot be used to justify a grouping in a phylogenetic classification. Two of these offending genera (neither from the Nearctic Region) are *Mannheimsia* Beyer (1965) and *Phlebothrix* Borgmeier (1969), both of which must be transferred to the Metopininae.

9 Tergite 8 present in female abdomen.

As discussed above in the groundpattern states of the female abdomen, tergite 8 is lacking from females of *Sciadocera*. The absence, and later re-occurence of this sclerite may be an example of an atavistic character state.

10 Posterior scutellar setae shorter and thinner than anterior scutellar setae.

This is another character that is lacking from most of the descendant taxa of the group it defines. All taxa with this character state were not included in this analysis, since most occur outside of the Nearctic Region. Schmitz (1939) proposed this character state as a defining trait of the tribe Beckerinini, a view that can be supported no longer. Perhaps the suppression of the primitive state of this character (anterior scutellar setae shorter and thinner than posterior scutellar setae) in at least two lineages of metopinines, and its later re-expression, is an example of another atavism.

3.7 Classification

This classification depicts the relationships of the taxa using sequencing and subordination (see also Fig. 3.5). Taxa equally indented are adelphotaxa; when there are more than one such group they are successive adelphotaxa, unless labelled *sedis mutabilis* (Wiley, 1981).

Family PHORIDAE
  subfamily HYPOCERINAE

  subfamily PHORINAE

  subfamily AENIGMATIINAE *sedis mutabilis*
    tribe Aenigmatiini
    tribe Diplonevrini

  subfamily CONICERINAE *sedis mutabilis*

  subfamily METOPININAE *sedis mutabilis*
    Triphleba Rondani
    Rhopica Schmitz

Beckerina Malloch

other metopinines

3.8 Justification of monophyletic subfamilies

Below the subfamilies of the Phoridae are briefly justified with constitutive (=autapotypic) features. Further discussion of these groups, with phylogenetic revisions of their included taxa, are subjects too extensive to be discussed here. They will be presented in future works, all of which are in manuscript.

3.8.1 HYPOCERINAE Lioy 1864

Type genus: *Hypocera* Lioy 1864

Constitutive features

1 Wing vein M_1 curved basally (Fig. 3.4D, less developed in this species than in most hypocerines).

2 Male terminalia symmetrical (Figs. 3.4A-B).

3 Surstyli absent or fused to epandrium of male terminalia of all genera except *Burmophora*, which has both surstyli separate (Figs. 3.4A-B).

4 Hypandrium with ventrally directed outer lobe (Figs. 3.4A-B).

5 Tergite 8 present in female ovipositor.

6 Wing vein R_s setulose (Fig. 3.4D).

This character state may not be a valid synapotypy at this level, as some members of other subfamilies also have this character state present.

Included Nearctic Region taxa. Abaristophora Schmitz, *Borophaga* Enderlein, *Burmophora* Beyer, *Hypocera* Lioy, *Stichillus* Enderlein.

This is a well-supported, monophyletic group that has been recognized for a long time (e.g. Schmitz, 1939), but not formally named or characterized.

Examination of a paratype male of *Burmophora comans* Beyer from Burma shows that the species formerly classified in the Holarctic Region genus *Crinophleba* Borgmeier (Borgmeier, 1967; Brown, 1990; Gotô, 1983) should be placed in *Burmophora* Beyer. *Crinophleba* Borgmeier is therefore a junior subjective synonym (**syn. n.**) of *Burmophora*. The affected taxa are *B. angustifrons* (Gotô) (Japan), *B. rostrata* (Borgmeier) (Canada) and *B. vitrinervis* (Malloch) (North America), all **comb.n**. Gotô (1983) had suggested previously that *Crinophleba* seemed to be related to *Burmophora*, but could not come to a definite conclusion because, according to him, the female of *Burmophora* was unknown. Females, however, were mentioned briefly in the original description of *Burmophora* (Beyer, 1958), but the elongate proboscis of the female, an important character state that shows the correct relationship between *Burmophora* and *Crinophleba*, was not mentioned.

3.8.2 PHORINAE Rondani 1856

Type genus: *Phora* Latreille 1796.

Notes about synonymy. This taxon formerly referred to all phorids that did not belong to the subfamilies Aenigmatiinae, Alamirinae, Metopininae, Termitoxeniinae or Thaumatoxeninae.

Constitutive features

1 Right hypandrial lobe enlarged, in most species with two processes, left hypandrial lobe reduced in many species (Fig. 3.4E).

2 Epandrium with long process (in most species this structure is the right surstylus) that articulates with enlarged right hypandrial process.

The left or right surstylus and the right hypandrial lobe of males of these genera seem to be developed as opposing grasping structures. The function of the male terminalia in Phoridae is unknown, but see the discussion about their evolution below.

Included Nearctic Region taxa. Anevrina Lioy, *Phora* Latreille, *Chaetopleurophora*

Strobl, *Coniceromyia* Borgmeier, *Spiniphora* Malloch.

3.8.3 AENIGMATIINAE Schmitz 1926

Type genus: *Aenigmatias* Meinert 1890

Constitutive features

1 Female with lateral sclerites on abdominal segment 7 (Figs. 3.4G-H).

2 Hind tibia with one or more dorsal, longitudinal rows of enlarged setulae (Fig. 3.3E, e).

3 Wing veins R_{2+3} and R_{4+5} subparallel (Fig. 3.4F).

Phylogenetic Relationships. The monophyly of the Aenigmatiine, in the previously defined, restricted sense, was challenged recently (Brown, submitted). Of the five Neotropical genera, all but one were found not to belong in a monophyletic group with *Aenigmatias*.

More recently, it has become clear that the genera *Dohrniphora*, *Diplonevra*, *Hypocerides* Schmitz, and related taxa (here placed in a newly resurrected tribe Diplonevrini Enderlein) belong in a monophyletic group with members of the Aenigmatiinae in the former, restricted sense. The newly recognized taxon containing the former Aenigmatiinae is here named tribe Aenigmatiini Schmitz. This taxonomic revelation was based on the discovery of a female specimen of an undescribed aenigmatiine (*Synaptophora critica* **gen. n., sp. n.**; described below) that bore several primitive characters for the group, namely fully developed wings, large tibial setae, and a full complement of frontal setae. In spite of these primitive characters, the specimen displays the defining characters states found in other Aenigmatiini, including the type genus *Aenigmatias*. This specimen had well developed sclerites present laterally on the female ovipositor, a shared, derived character also found in at least the genera *Diplonevra* (some species only), *Dohrniphora*, *Dicranopteron* and *Myopiomyia*. Although the lateral sclerites are absent from other members of the Aenigmatiini that I examined, this is attributed to the further modification and shortening of the female terminalia. This character state is also absent from female specimens of *Hypocerides aetherus* Schmitz and most (but not all) species of *Diplonevra*.

The females of the phorine genus *Spiniphora* also have lateral sclerites on the female ovipositor, although they are formed somewhat differently. I am reluctant, however, to propose a monophylum based on the Phorinae + Aenigmatiinae because there are no other synapotypies to support this relationship. Furthermore, since males of at least *Aenigmatias* have surstyli fused to the epandrium, it seems likely that the Aenigmatiinae are a relatively more derived group, more closely related to the Conicerinae and the Metopininae.

Hennig (1973) stated that members of the aberrant, Old World subfamily Thaumatoxeninae were probably only highly derived Aenigmatiinae (Aenigmatiini of this review). A recent discovery of a relatively primitive female thaumatoxenine from

Thailand (unpublished information) supports this view; the specimen has fully developed wings and, more importantly, large tibial setae which are arranged in a pattern that resembles the setal pattern of *Synaptophora critica*.

Included Nearctic Region Taxa. Tribe Diplonevrini: *Diplonevra* Lioy, *Dohrniphora* Dahl and *Hypocerides* Schmitz. Tribe Aenigmatiini: *Aenigmatias* Meinert.

SYNAPTOPHORA gen. n. (not Nearctic)

Type species: *Synaptophora critica* (present designation)

Derivation of generic name. From the Greek *synaptos*, meaning to bind together, referring to the union of the former Aenigmatiinae with the Diplonevrini based on the single known specimen of this genus.

Diagnosis. Limuloid female with complete frontal setation and well developed wings; abdomen with lateral sclerites on segments 7 and 8. Tibiae with large setae.

***Synaptophora critica* sp. n.**

Derivation of species name. From the Latin *criticus*, meaning capable of judging, referring to our ability to link the Aenigmatiini with the Diplonevrini, based on this specimen.

Description (female only; male unknown). Body length 1.9mm. Head and abdomen brown, thorax ferruginous, coxa and femur yellow, tibia and tarsomeres dark. Frontal furrow absent. Frons with one pair divergent, upwards pointing supra-antennal setae, one pair parallel supra-antennal setae and 4-4-4 frontal setae. Eye reduced. Ocelli present. Flagellomere 1 orange, round. Palpus orange, with large setae. Mouthparts reduced, probably vestigial. Prothoracic spiracle dorsal. Anepisternum undivided, bare. All legs stout, broad; hind femur greatly enlarged. All femora with enlarged dorsal, apical setae. All tibiae and tarsomeres with long setae which lay flat on the segment and appear as longitudinal ridges with light microscopy (Figs. 3.3E-F); tibiae with the following projecting setae- fore tibia with five equally spaced, anterodorsal setae, mid tibia with basal pair (one anterodoral and one posterodoral) of setae and two smaller, posterodorsal setae, hind tibia with one dorsal, longitudinal row of enlarged setulae, row of several anterodorsal and row of several posterodorsal setae, and row of five pre-apical anteroventral setae (Fig. 3.3F). Wing slightly reduced, but major veins present (Fig. 3.4F). Wing vein R_{2+3} subparallel to vein R_{4+5}. Halter yellow. Abdomen with tergite 5 narrow, tergite 6 absent. Ovipositor short, intersegmental areas reduced. Segments 7 and 8 with lateral sclerites (Fig. 3.4H). Terminal tergites of ovipositor, including cerci, fused. Ventral valve of ovipositor bilobed.

Way of life and immature stages. Unknown. Based on the limuloid body structure, this fly probably lives in ant or termite colonies.

Phylogenetic relationships. This fly has many primitive character states, as discussed above. Less primitive states of many of these characters are found in other Aenigmatiini; for instance females of *Euryphora* Schmitz retain a single pair of large, supra-antennal setae (Schmitz, 1915, Fig. 11), some genera (*Euryphora* and *Aenigmatopoeus* Schmitz for instance) have large tibial setae (Schmitz, 1915, Fig. 15; Colyer, 1958, Figs. 16, 17) and females of many genera have wing rudiments.

The sub-parallel wing veins R_{2+3} and R_{4+5} in this specimen, as well as the presence of lateral sclerites on segments 7 and 8, and a single dorsal, longitudinal row of enlarged setulae are character states similar to those found in adults of the genus *Dohrniphora.* If the phylogenetic hypothesis of close relationship between the Aenigmatiini and Diplonevrini is accepted, these similarities must represent groundpattern conditions for the Aenigmatiinae. The alternatives are to dismiss these similarities as having been developed in parallel, with no special relationship between Aenigmatiini and Diplonevrini supported; or to take the aenigmatiine characters of *Synaptophora* as convergent with other Aenigmatiini, again with no special relationships between the two tribes. I believe that the aenigmatiine characters of *Synaptophora,* however, are too numerous to dismiss as convergence. Specifically they are: reduction of the eye; flattened head, thorax and abdomen; prothoracic spiracle dorsal; legs stout, with large setae; ovipositor shortened, with tergites of last segments, including cerci, fused. Similarly, parallel development of lateral sclerites on the female ovipositor and the subparallel radial wing veins seems unlikely. The discovery of a male specimen of this genus would be extremely illuminating.

Holotype, ♀ (abdomen, one hind leg dissected), UGANDA: Entebbe, 11.ii.1972, in forest (*Falke*) (CNC).

3.8.4 CONICERINAE LIOY 1864

Type genus: *Conicera* Meigen 1830

Constitutive features

1 Flagellomere 1 of male elongate, conical.

2 Frons short.

Further analysis of this newly proposed subfamily must await future studies, but at least the following genera belong to this group: *Ceratusa* Borgmeier, *Conicera* Meigen (widespread), *Contopteryx* Schmitz (south Chile, south Argentina), *Darwiniphora* Schmitz (south Chile), *Gymnoptera* Lioy (worldwide), and an undescribed genus from New Zealand.

The defining character states of this group have evolved more than once in the history of the Phoridae, but since all of the taxa named above have both surstyli fused to the epandrium, postulating for them an independent evolution of elongate flagellomere 1 is not parsimonious.

Included Nearctic Region taxa. Conicera Meigen.

3.8.5 METOPININAE RONDANI 1856

Type genus: *Metopina* Macquart 1835

Constitutive features

1 Hypandrium with basal setae.

2 Anepisternum furrow present.

The anepisternal furrow in many species of *Triphleba* is faint or absent.

Although detailed phylogenetic analysis of this group is deferred until a later publication, it should be noted that the tribe Beckerinini, which includes among other genera *Rhopica* and *Beckerina*, is shown here to be paraphyletic. Justification for this tribe was based on the presence of reclinate or porrect supra-antennal setae, character states which are primitive with respect to the Hypocerinae, Phorinae, Aenigmatiinae, Conicerinae and *Triphleba*. Since Beckerinini is paraphyletic as currently defined, it should not be used to group its formerly included genera within the classification of the Phoridae. Furthermore, since there at least three primary divisions of the Metopininae (*Triphleba, Rhopica* and *Beckerina*) before the "other Metopininae" are encountered, the tribe Megaseliini Disney (1989) is ranked at too high a level, unless one wishes to propose at least new tribes for *Triphleba* and *Rhopica*. Such a proliferation of new names would not be acceptable, especially since other former beckerinine taxa can be expected to require further categories when eventually included in this system.

Included Nearctic Region taxa. The many metopinine genera are listed in Peterson (1987) and Brown (1988); to these must be added the genus *Triphleba* Rondani.

3.9 Evolution of the male genitalia in Phoridae

Much of the above phylogenetic hypothesis is based on interpretation of the male terminalia. Accordingly, I offer the following observations on their evolution. Most of these interpretations are speculative, as no studies have been performed on the musculature or function of phorid terminalia.

In the Hypocerinae, the most primitive terminalia are found in *Burmophora*, males of which have a pair of symmetrical surstyli possibly used to hold the female abdomen during copulation. Individuals in other hypocerine genera have lost these surstyli, but have ventral processes on the hypandrium that may be used for a similar function.

In the Phorinae, males of species of the genus *Phora* have a separate right surstylus and a (sometimes narrowly) fused left surstylus (extensively illustrated by Gotô, 1984, 1985c, d, e, 1986). In males of some other phorines, such as *Anevrina*, the basic pattern has been complicated by folds and extensions of these structures, as well as those of the subepandrial plate (=sternite 10, interparameral sclerite, intergonocoxal sclerite, intergonopodal sclerite). In opposition to the left surstylus, the right hypandrial lobe has become enlarged and in males of most genera, bilobed. Presumably, this results in a more efficient clasping mechanism, but functional aspects of these structures are unknown.

In the Aenigmatiinae, male individuals of most genera have no discernible surstyli, or they are fused to the epandrium. An exception is found in males of the genus *Aenigmatias*, which have surstyli similar to those of other phorids, fused to the epandrium.

Adult males of Conicerinae have terminalia which do not suggest relationship to any other phorid group. The surstyli are elongate in males of some genera, and fused to the epandrium. The hypandrium has a pair of large, subequal processes, one on each lobe.

In the Metopininae, males of the genera *Triphleba* and *Rhopica* retain a primitive type of male terminalia, with the extensive anterior fusion of the epandrium and hypandrium. The surstyli are large, but fused to the epandrium. In *Beckerina* and other relatively more derived taxa, the surstyli are reduced in individuals of most taxa; exceptions occur, for instance in *Gymnophora*, subgenus *Cerocratia* (Brown, 1987a). In these instances, however, it is probably impossible to determine without further phylogenetic data whether the elongate "surstyli" are in fact retained surstyli or neomorphic processes of the epandrium. In most Metopininae, there is little evidence of obvious clasping structures, such as the surstyli of *Burmophora*, Phorinae, and others.

3.10 Implications and limitations of the phylogenetic analysis

My interpretation of the groundpattern character states discussed above differs markedly from that of Disney (1988). Most of these states are distributed sporadically throughout the subfamilies; for instance a two-segmented palpus is present in individuals classified as Aenigmatiinae and Metopininae, tibial setal rows are found in individuals of some genera of the Hypocerinae, Aenigmatiinae and Metopininae, and a median frontal furrow is present in adults of some genera of Phorinae, Conicerinae and Metopininae. Within these subfamilies, other characters indicate that these structures are newly evolved in each lineage and thus cannot be part of any groundpattern of the family as a whole, unless they exist as an underlying synapotypy.

This new classification undoubtedly will be modified by further research, and discovery of taxa which will not fit into any of the named groups. I believe, however, that this classification reflects a conservative first approximation to the correct phylogeny of the Phoridae. If the relatively tenuous character states of the fusion of male surstyli to the epandrium are not accepted as adequate indicators of phylogenetic relationship, a less resolved tree (Fig. 3.5B) could be proposed. In the absence of further evidence, however, I support the more resolved tree (Fig. 3.5A).

The major advance made possible by the rigorous use of the Sciadoceridae and Ironomyiidae as outgroups is the realization that the former subfamily Phorinae and the metopinine tribe Beckerinini are paraphyletic. More logical relationships for the constituent taxa of these groups have been shown, with the recognition of the Hypocerinae, Phorinae, Aenigmatiinae, and Conicerinae, and the inclusion of *Triphleba* within the Metopininae. Hopefully, this analysis will encourage further investigations into higher classification of the Phoridae, based on new character states, such as those found in the study of internal adult structure, and internal and external larval structure. Then, perhaps, genera which do not fit in any recognized group will be classified properly.

3.11 Acknowledgments

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TABLE 3.1 Distribution of plesiotypic and synapotypic character states among Sciadoceridae, and subfamilies and selected genera of Phoridae. 0 - plesiotypic state, 1 - apotypic state, ? - unknown or equivocal.

Characters	1234567890
Taxa	
Sciadoceridae	0000000000
Hypocerinae	1001100010
Phorinae	1101100000
Aenigmatiinae	1111100000
Conicerinae	1111100000
Triphleba	1111110000
Rhopica	11111??101
Beckerina	1110011111
other Metopininae	1110011110

Fig. 3.1. A-B. Head, frontal. A, *Diplonevra nitidula* (Meigen); B, *Megaselia* sp.; C-D. Thorax, lateral. C, *Phora* sp.; D, *Megaselia* sp.; E, *Diocophora appretiata* Schmitz, male terminalia, ventral; F, *Dohrniphora gigantea* (Enderlein), hind tibia, posterodorsal. Abbreviations: a - anepisternum, af - anepisternal furrow, b - basal setae of hypandrium, e - row of enlarged setulae, sa - supra-antennal setae.

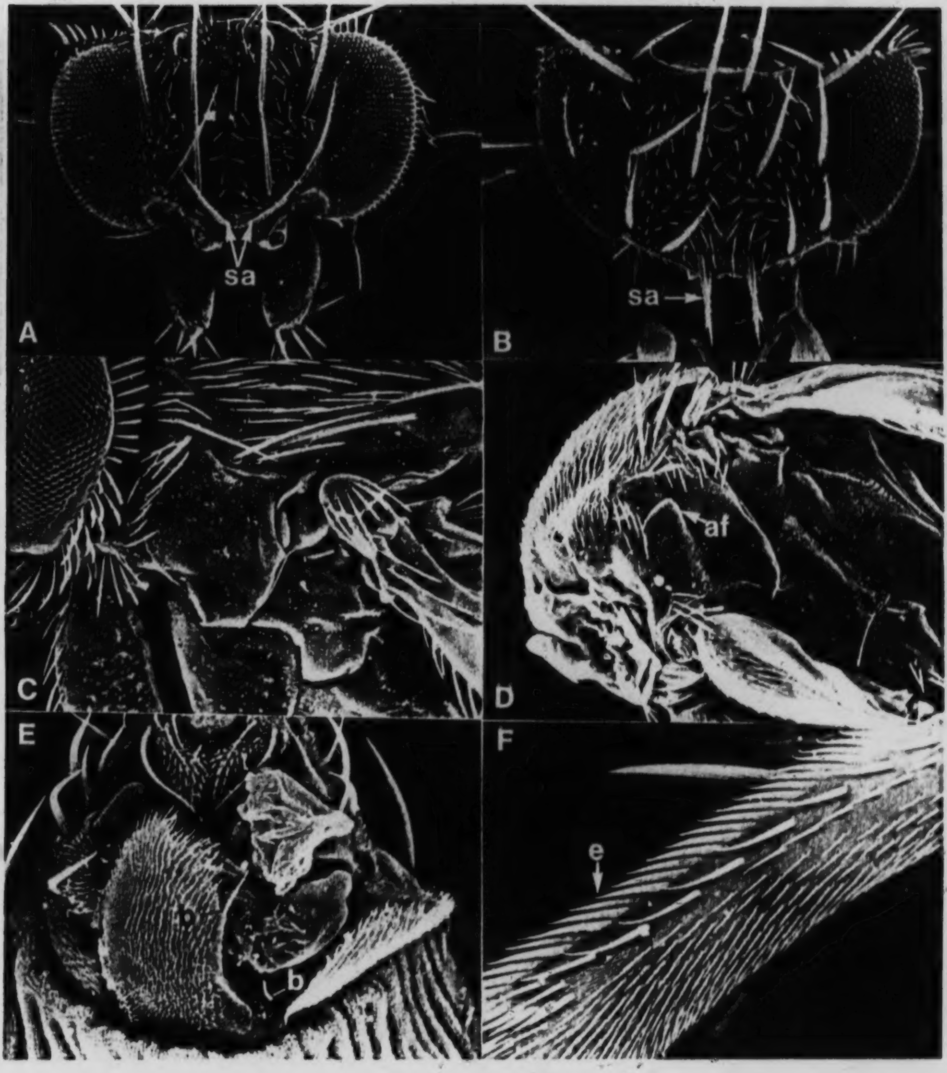

sa
A
sa
B
C
af
D
E
b
b
F
e

Fig. 3.2. A-F. Frons, low magnification, high magnification. A-B, *Gymnophora luteiventris* Schmitz; C-D, *Triphleba labida* Borgmeier; E-F, *Conicera* sp. Abbreviations: f - frontal furrow, p - pore.

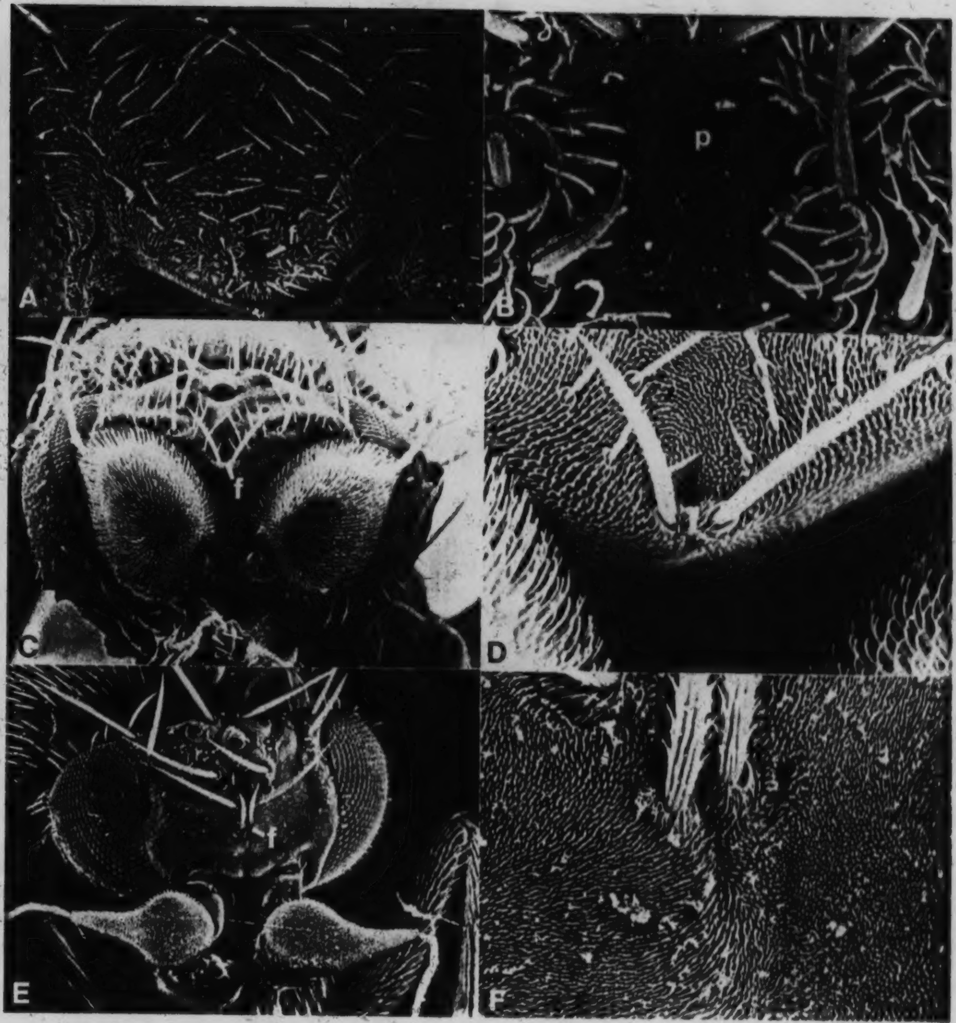

A
B
p
C
f
D
E
f
F

Fig. 3.3. A-D. Frons. *Agathomyia* sp., Platypezidae; B, ditto, higher magnification; C, *Sciadocera rufomaculata* White; D, *Lonchoptera* sp.; E-F. *Synaptophora critica* sp. n., hind tibia. Abbreviations: f - frontal furrow, e - row of enlarged setulae, t1 - basal tarsomere.

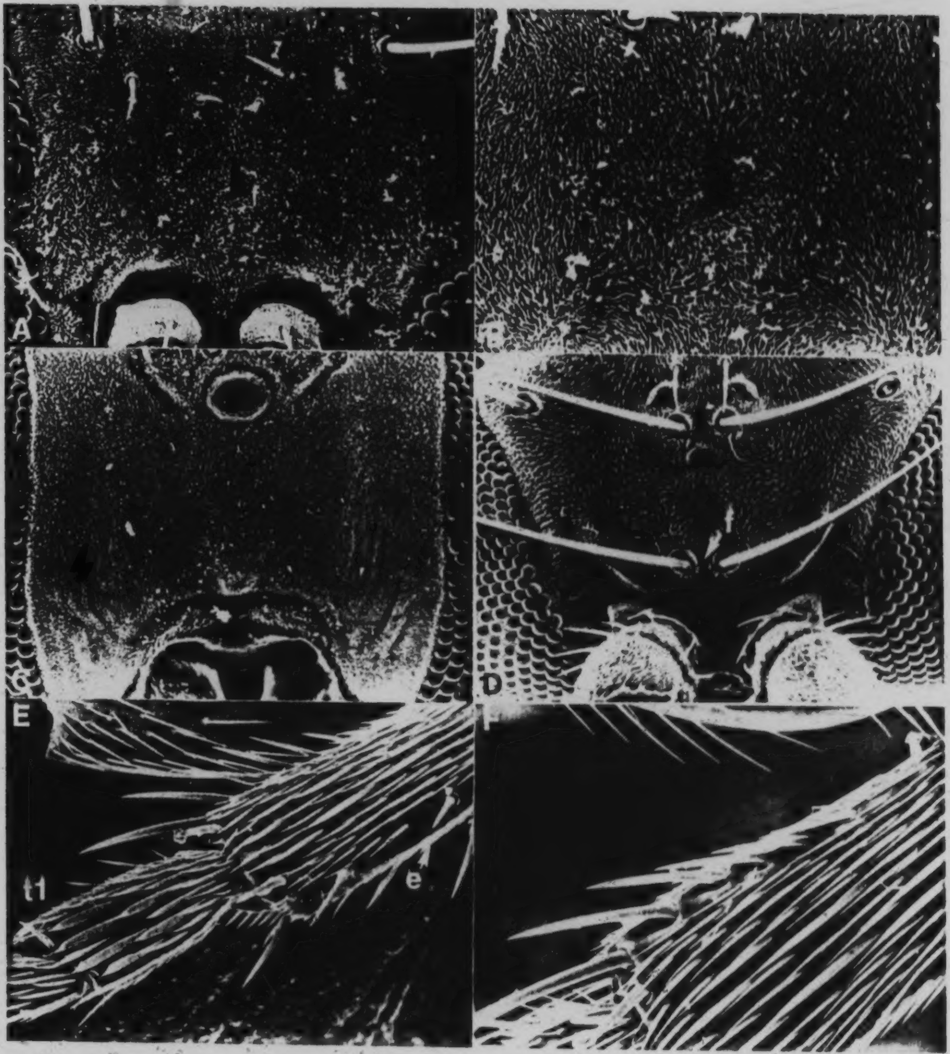

A
B
C
D
E
F
t1
e

Fig. 3.4. A-B. *Burmophora comans* Beyer, male terminalia. A, left lateral; B, right lateral. C, *Diocophora* sp., male terminalia, left lateral; D, *Peromitra* sp., wing; E, *Spiniphora spinulosa* (Malloch), hypandrium, ventral; F, *Synaptophora critica* sp. n., wing; G, *Dohrniphora* sp., female abdomen, ventral; H, *S. critica*, female abdomen, dorsal. Scale bar = 0.1mm. Figs A-C, E to same scale, Figs. D, F, G-H to same scale. Abbreviations: e - epandrium, h - hypandrium, l - left process of hypandrium, ls - lateral sclerite, r - right process of hypandrium, s - surstyli.

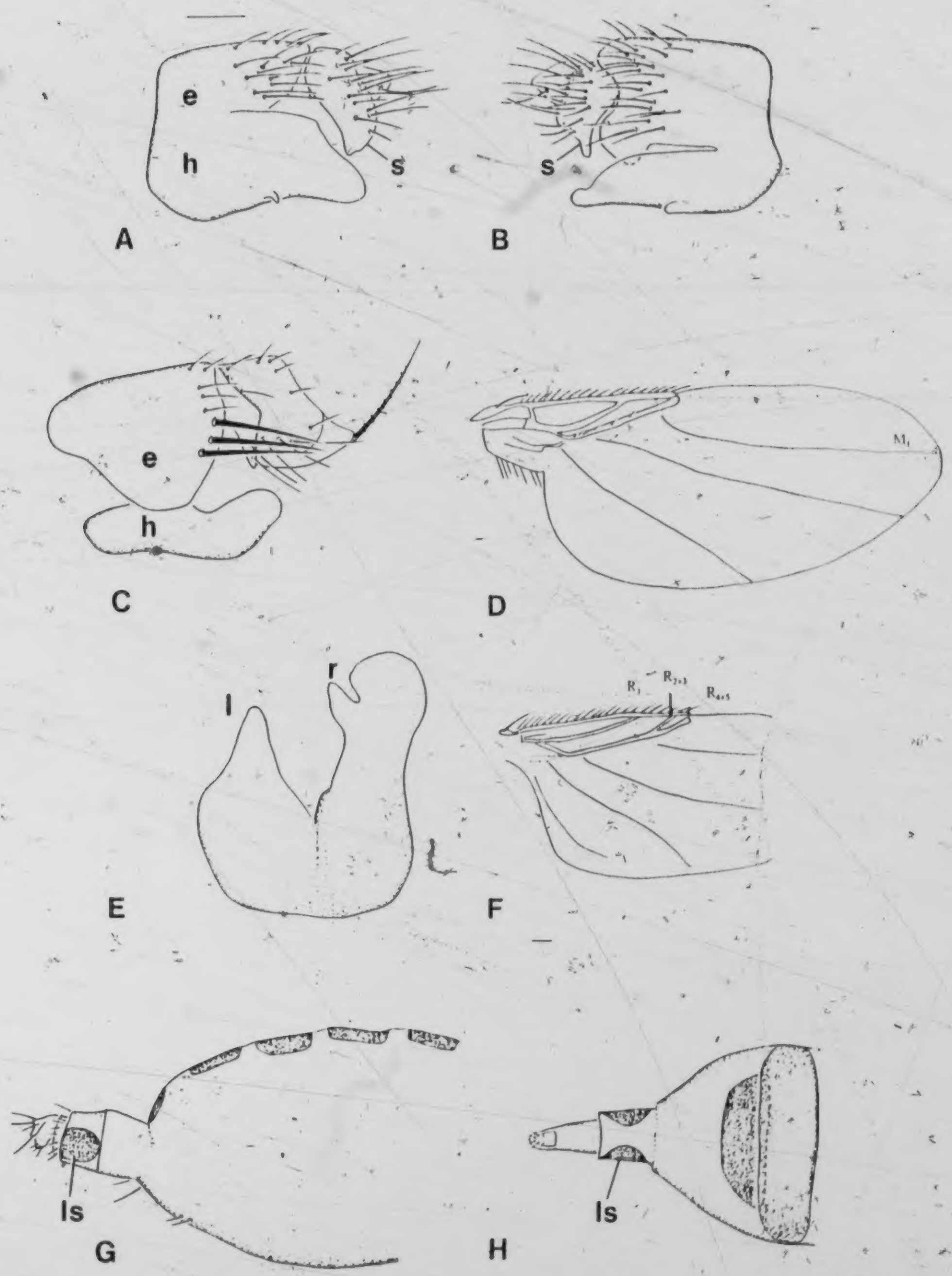
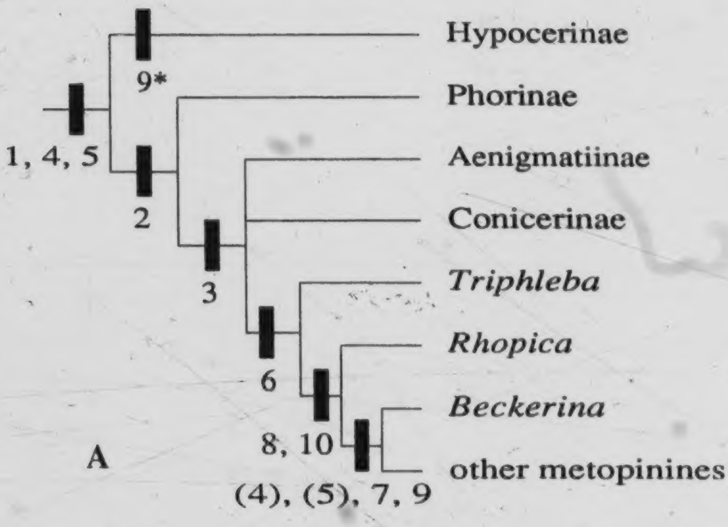
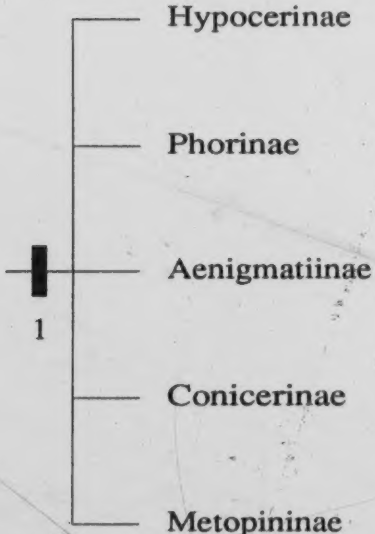

e
h
s
s
A
B
e
h
C
M1
D
r
l
E
R1
R2+3
R4+5
F
ls
G
ls
H

Fig. 3.5. Cladograms of relationships of the Phoridae. Character states with asterisks are homoplastic, those in parentheses are reversals. A, most resolved tree; B, least resolved tree.


Hypocerinae
9*
Phorinae
1, 4, 5
Aenigmatiinae
2
Conicerinae
3
Triphleba
Rhopica
6
Beckerina
8, 10
other metopinines
(4), (5), 7, 9

A


Hypocerinae
Phorinae
Aenigmatiinae
1
Conicerinae
Metopininae

B

3.12. References

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4. REVISION AND PHYLOGENETIC CLASSIFICATION OF THE GENERA OF SUBFAMILY HYPOCERINAE (DIPTERA: PHORIDAE)

4.1 Introduction

The subfamily classification of the Phoridae has been revised recently (Chapter 3), and the genera reassigned to monophyletic groups. The relatively most primitive of these groups is the subfamily Hypocerinae Lioy, a group of worldwide distribution. Their relatively large size and dark color makes them conspicuous members of the European fauna, and hypocerines were well known to early workers such as Meigen (1830), Macquart (1835) and Lioy (1864). The close relationships among these genera were recognized first by Schmitz (e.g. 1929), who called them the *Borophaga*-group of genera. Although he was aware that these flies formed a natural group, Schmitz did not propose a formal name for them. Of the presently recognized members of this subfamily, Schmitz recognized the proper relationships of all but one: *Burmophora* Beyer, described shortly before Schmitz's death in 1960.

The following revision is an attempt to organize the included genera into monophyletic groups. Species level revisions of all genera are needed to progress further, but this generic treatment should set the groundwork for future studies.

4.2 Materials and methods

Material was examined from the following collections, the names of which are preceded by a coden, used as an abbreviation for reference to these collections (names of curators in parentheses).

BVB	Collection of the author
CNC	Canadian National Collection, Biosystematics Research Centre, Agriculture Canada Central Experimental Farm, Ottawa, Ontario, Canada K1A 0C6 (J.M. Cumming)
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 150-164, D-5300, Bonn 1, Germany (H. Ulrich)

Taxa from outside of the Nearctic Region frequently were used for comparison and to test hypotheses based on Nearctic specimens. Because of our limited knowledge about the Neotropical, Oriental, Australasian and Afrotropical phorid faunas, many of the species from these regions were not identified to species. This is in recognition of the incomplete coverage given by existing keys, as well as the realization that there are a great many undescribed species in regions outside of North America and Europe.

Full taxonomic synonymies are not given in this paper, except for those not found in Borgmeier (1968, 1971).

Male terminalia were examined by treatment in hot 10% KOH, and rinses of 30%

acetic acid, water, and alcohol. They were then placed in an evaporating dish with a drop of glycerine and about 2ml of alcohol, and were put on a warming tray to allow the alcohol to evaporate. Terminalia were then placed in glycerine jelly on glass slides and examined with light microscopy.

Some specimens were gold-coated and examined with a Cambridge 100 Scanning Electron Microscope.

Hypothesized relationships were reconstructed using standard cladistic techniques (Hennig, 1966). The cladogram in this paper was constructed manually, without computer algorithms. The data set was subsequently checked with the computer program Hennig-86 (Farris, 1989) to see if there were further equally parsimonious cladograms.

4.3 Terms

Recent reviews of Diptera phylogeny have postulated adelphotaxon (Griffiths, 1972), ancestor-descendant (Chvála, 1983) or no special relationship (McAlpine, 1989) between the Orthogenya and Cyclorrhapha. This disagreement affects the terms used to refer to the male genitalia, and I deal with it as I have previously (Brown, 1987).

The terms synapotypic, apotypic, plesiotypic etc. have been used in this paper as more general terms, rather than synapomorphic, apomorphic, plesiomorphic and so on that refer only to structure (Chapter 2, Terms). Other terms not used by Hennig, but subsequently proposed by Ax (1987) are used in this work: adelphotaxon (=sister-group) and groundpattern (=groundplan). The reasons for preferring the use of these more recent terms are those of Ax (1987).

4.4 Reconstructed phylogeny of Hypocerinae

Cladograms (Figs. 4.8-4.9) were constructed based on the hypothesized synapotypic character states discussed below (see also Table 4.1). These cladograms are two of twenty-eight equally parsimonious trees for these data, as analyzed by Hennig-86. The variations of this tree revolve around the New Zealand hypocerines *Bothroprosopa*, *Palpocrates*, *Tarsocrates* and *Tonnoiriophora*. Data are absent for character state 4 from *Palpocrates* and *Tarsocrates*; if we assume that this character state is actually present in these taxa, only four trees remain. These four trees reflect the character conflict between character states 4 and 5. I consider character state 5, loss of wing vein R_{2+3}, more likely to arise convergently than character state 4, gain of tergite 7. If character state 4 is weighted higher than state 5, two equally parsimonious cladograms remain (Figs. 4.8-4.9).

Hypothesized synapotypic character states.

1) Surstyli lost or fused to epandrium (Figs. 4.4D-G, 4.5A-G, 4.6A-F).

2) Inner lobe of hypandrium 1) reduced (Figs. 4.4B-C) or 2) lost.

3) Epandrium continuous below cerci (Fig. 4.3C).

4) Tergite 7 present in females.

This tergite is present in females of *Sciadocera*, but absent from females of *Burmophora* and most other primitive-grade phorids. Therefore, this tergite is newly-derived in the New Zealand endemic genera *Tonnoiriphora* and *Bothroprosopa*, and supports their inclusion in a monophyletic taxon. This character state is unknown for *Ceratoplatus*, *Palpocrates* and *Tarsocrates*, other New Zealand endemic taxa, but the similarities between the male terminalia of at least *Palpocrates* and *Tarsocrates* with those of *Tonnoiriphora* and *Bothroprosopa* make it likely that these genera also belong in this monophyletic group.

5) Wing vein R_{2+3} reduced or absent (Figs. 4.7A, C-F).

This vein is absent from wings of most species of hypocerines, except the most basal genera, but there is a faint, vestigial vein R_{2+3} in some adults of *Peromitra* and *Borophaga*, and a well developed R_{2+3} in adults of *Godavaria*.

6) Hind tibia with enlarged setulae (Figs. 4.1F, 4.2A-C).

Individuals of most genera except *Hypocera* have these setulae organized into dorsal, longitudinal rows.

Although Disney (1988) has proposed that the presence of longitudinal rows of setulae on the hind tibia is primitive in the Phoridae, the outgroup evidence is based only on one species of Platypezidae with slightly enlarged setae (see Chapter 3).

7) Anepisternum setulose (Fig. 4.3B).

This character state was discussed previously (Chapter 3).

8) Flat spinuli present on hypandrium (Figs. 4.1C-E).

Most Phoridae have only scattered or dense setulae on the hypandrial lobes.

9) Vertex with raised lip (Fig. 4.1B, r).

A raised, posterodorsal lip on the vertex is found in *Hypocera*, and most *Borophaga*-group species, but not in the one male specimen of the genus *Trineurocephala* that I was able to examine. The head of male *Trineurocephala*, however, is highly modified, with a greatly narrowed frons. This modification could have affected the expression of the lip.

10) Aedeagal apodeme elongate (Figs. 4.6D-E).

11) Supra-antennal setae absent (Fig. 4.1A).

The outgroup taxon Sciadoceridae also lacks these structures, but their presence in adults of the relatively more primitive hypocerines (*Burmophora*, *Tonnoiriphora*, *Bothroprosopa* and *Hypocera*) means that they have been lost secondarily in the *Borophaga*-group.

12) Subcercal area of epandrium expanded, especially on right side (Fig. 4.3C).

13) Female proboscis elongate, geniculate; frons produced anteriorly between antennae (Brown, 1988, Fig. 130).

14) Male flagellomere 1 elongate, pointed (Schmitz, 1939, Fig. 2).

15) Apical tarsomere on male foretarsus flattened, broad; pulvilli broad (Figs. 4.2D-F).

Males of some species of *Stichillus* and *Peromitra* have less flattened tarsomeres, possibly a reversal of this state. Some species of *Peromitra* lack this character state altogether, as do outgroup taxa (Fig. 4.3A). This represents either a loss in these species of *Peromitra*, or shows that this character state is unreliable.

16) Aedeagus tube-shaped (Fig. 4.6D).

The aedeagus of the outgroups of the Phoridae, the Ironomyiidae and Sciadoceridae, is somewhat similar to this state. This is not a reversal, however, but a modification of the basic, multi-articled aedeagus.

17) Male with sternites on segments 5 and 6.

The male *Trineurocephala* I examined, and males of some *Stichillus* species have both sets of sternites, but other species of *Stichillus* have only the pair on segment 6. Possibly, the sternites of segment 5 have been lost in these species. Some species have a single sclerite instead of a pair.

4.5 Classification

The genera of this subfamily are treated below, in phylogenetic order, based on the following partially sequenced classification (conventions as in Wiley, 1981). I used the cladogram from Fig. 4.8 for this classification, as it is more conservative in the proposal of groupings. The cladogram in Fig. 4.9 proposes a group including *Palpocrates*, *Tarsocrates* and *Tonnoiriphora* based on a reversal of character state 5. Such a grouping is premature, and will remain so until these groups are revised.

SUBFAMILY HYPOCERINAE LIOY

***Burmophora* Beyer**

***Bothroprosopa*-group**

- ***Tonnoiriphora* new genus** *sedis mutabilis*
- ***Bothroprosopa* Schmitz** *sedis mutabilis*
- ***Palpocrates* Schmitz,** *sedis mutabilis*

Tarsocrates* Schmitz, *sedis mutabilis

Hypocera Lioy

Borophaga- group

Borophaga- subgroup

Borophaga* Enderlein, *sedis mutabilis

Godavaria* new genus, *sedis mutabilis

Latiborophaga* new genus, *sedis mutabilis

Abaristophora- series, ***sedis mutabilis***

***Antipodiphora* Schmitz**

***Abaristophora* Schmitz**

Stichillus- subgroup

Peromitra* Enderlein, *sedis mutabilis

Stichillus* Enderlein, *sedis mutabilis

Trineurocephala* Schmitz, *sedis mutabilis

Ceratoplatus Schmitz, *incertae sedis*

4.6 Revision of genera

SUBFAMILY HYPOCERINAE LIOY 1864

Type genus: *Hypocera* Lioy 1864

Notes on nomenclature. The name Hypocera has been used as a supra-generic taxon that included some Phoridae for many years, at least since Macquart (1835). This name, however, was not based on a type genus, as *Hypocera* Lioy was described well after this time. Therefore, Lioy (1864) is the first use of the name *Hypocera* Lioy as the type of a family-group name.

Diagnosis. Generally dark-colored, robust flies. Wing vein R_s setulose, vein M_1 curved basally. Male terminalia symmetrical. Surstyli absent or fused to epandrium in male terminalia of all genera except *Burmophora*, which has both surstyli separate. Hypandrium with ventrally directed outer lobe. Female abdomen lacks tergite 7, except for *Bothroprosopa* and *Tonnoiriphora*, both of which have tergite 7 present; entire segment 7 slightly sclerotized in most species; tergite 8 present.

Geographic distribution. Found world-wide.

Chorological affinities. Members of this group are particulary well represented in New Zealand, where several endemic genera exist. The New Zealand phorid fauna in general is primitive, with few members of the more derived lineages of phorids (Metopininae) present. In contrast, hypocerines are nearly absent from the Neotropical Region (an area of great diversity of Metopininae), the only exceptions being seven described species of *Stichillus*, three species of *Trineurocephala* and two species of *Latiborophaga*. Apparently, the *Borophaga*-group lineage gained access to the Neotropical Region relatively recently, giving rise to several species but only one new genus.

Phylogenetic relationships. This subfamily is the most basal of the extant Phoridae. Adult males of *Burmophora* have completely separate left surstyli, a primitive character that is shared only by some Alamirinae (Disney, 1981, 1990).

The presence of symmetrical male genitalia cannot be regarded as a retained primitive character, reminiscent of the Lonchopteridae, Ironomyiidae and Platypezidae, as asymmetrical genitalia are found in Sciadoceridae and most other Phoridae; however, the terminalia and other characters of many hypocerines are indeed platypezid-like. Examples of platypezid-like characters found in some hypocerines, that here are considered convergent apotypies include the following: symmetrical male terminalia, tube-shaped aedeagus (Fig. 4.6D, a), form of the hypandrium (similar to some *Agathomyia* (Platypezidae)), sternites present on abdominal segments in male, and lack of supra-antennal setae.

For purposes of discussion, the taxa in this subfamily are arranged in one grade group, the primitive hypocerines (*Burmophora*, the *Bothroprosopa*-group and *Hypocera*), and two monophyletic groups, the *Stichillus*-subgroup (*Peromitra*, *Stichillus*, and *Trineurocephala*) and the *Borophaga*-subgroup (*Abaristophora*, *Antipodiphora*, *Borophaga*, *Godavaria* new genus and *Latiborophaga* new genus).

Known fossil material. As noted by Schmitz (1951), the Baltic amber fossil species *Dohrniphora transita* Brues (1923) probably belongs in the genus *Borophaga*. Additionally, and more remarkably, there are male specimens of *Antipodiphora* in the Dominican amber (Oligocene age) collection of B.V. Brown and D.H. Feener (BVB). Extant species of this genus are restricted to New Zealand.

The presence of species of hypocerine genera on New Zealand potentially could give clues to a minimum age of this taxon, if the time of isolation of the islands from the rest of the southern hemisphere continents could be known. The separation of New Zealand from Australia is usually thought to have begun in the late Jurassic, but as Briggs (1987) and Craw (1982) have pointed out, putting a date on this area may involve more complex considerations. Further geological, paleontological and biogeographic study of this region is needed to establish whether New Zealand is a composite (as Craw, 1982 maintains) or a single area, and at what time the fauna was isolated. If the late Jurassic date is accepted, the minimum age of the hypocerines would greatly predate other fossil evidence of the Phoridae and Sciadoceridae.

Similarly, the disjunct distribution of members of the genus *Latiborophaga* in Africa and South America provides suspiciously old dates. If this disjunction is correlated with the separation of the two continents during late Jurassic- early Cretaceous times (Briggs, 1987), the origin of *Latiborophaga*, and of the Hypocerinae, greatly predates phorid fossils. The Dominican amber fossil *Antipodiphora* provides a solution to this problem, however. The genus *Antipodiphora* was apparently much more widely distributed in the relatively recent past (25 million years ago), and its present restriction to New Zealand is a result of its extinction elsewhere. Similarly, members of *Latiborophaga* could have been widespread, until recent extinction events restricted their distribution to Africa and South America.

Included taxa. *Abaristophora* Schmitz (Holarctic Region), *Antipodiphora* Schmitz (New Zealand), *Borophaga* Enderlein (widespread), *Bothroprosopa* Schmitz (New Zealand), *Burmophora* Beyer (Holarctic and Oriental Regions), *Godavaria* new genus (Oriental Region), *Hypocera* Lioy (Holarctic and Oriental Regions), *Latiborophaga* new genus (Afrotropical and Neotropical Regions), *Palpocrates* Schmitz (New Zealand), *Peromitra* Enderlein (Palearctic and Oriental Regions), *Stichillus* Enderlein (widespread), *Tarsocrates* Schmitz (New Zealand), *Tonnoiriphora* new genus (New Zealand), and *Trineurocephala* Schmitz (Neotropical Region). According to Schmitz (1939), *Ceratoplatus* Schmitz also belongs to the Hypocerinae, based on the structure of the male terminalia.

4.6.1 *Burmophora* Beyer 1958

Crinophleba Borgmeier 1967, Goto 1983, Brown 1990

(Fig. 4.4A)

Type species: *Burmophora comans* Beyer 1958 (by monotypy).

Derivation of generic name. Named for the country (Burma) where the type species was collected.

Diagnosis. Female with elongate proboscis. Wing vein R_{2+3} present. Wing vein R_s setulose. Male with cerci absent (as in Gotô, 1983, Fig. 6; Brown, 1990, Figs. 2-3).

Way of life and immature stages. Larval and adult food are unknown. The only observation of life history are those of Gotô (1983), who noted that "*C. angustifrons* is widely distributed throughout Japan and appears in spring to early summer at the mountaneous regions. The male adults were observed hovering in swarms on herbaceous plants". Specimens of *B. comans* were also collected in a mountainous region, but *B. vitrinervis* is not restricted to high elevations in North America. One female specimen of *B. rostrata* in the Canadian National Collection was collected in the canopy of a tree on Mt. Rigaud, Quebec.

The structure of the immature stages is unknown.

Collecting methods. I have collected these flies only in Malaise traps.

Geographical distribution. Known from Burma, Japan, Canada, and northern USA.

Phylogenetic relationships. This genus is the adelphotaxon to all other examined Hypocerinae. In common with other Hypocerinae, *Burmophora* has a curved wing vein

M_1, and a small hypandrial process.

Hypothesized autapotypic character states of *Burmophora* include the following:

1 Female with elongate proboscis.

2 Male lacking cerci

Number of recognized species. Four.

Material examined. ***Burmophora comans*** **Beyer**, 1 paratype ♂, 1 paratype ♀: BURMA: N.E. Burma, Kambaiti, 2000m, 11-18.v.1934, Malaise trap (ZFMK); ***B. vitrinervis*** **(Malloch)**, CANADA: **Alberta**: Opal, 53°59'N, 113°13'W, 1♂, 20-22.vii.1989, B.V.Brown, Malaise trap, sand, jack pine (BVB), **Ontario**: Guelph, South Arboretum, 1 ♂, 11-16.v.1985, 1 ♂, 24-30.v.1985, 3♂, 19-24.vi.1985, 1♂, 6-10.viii.1985, Malaise trap, forest edge, 1♂, 7-11.vi.1985, Malaise trap, wet shrubby meadow, B.V.Brown (BVB), 3♂, Metcalfe, 10-11.v.1986, B.Cooper, Malaise trap (BVB), Stouffville, 2♂, 26.v.-2.vi.1985, B.V.Brown, Malaise trap (BVB).

Bothroprosopa-group

Diagnosis. Tergite 7 present in female ovipositor.

Remarks. Although the females of *Palpocrates* and *Tarsocrates* are unknown, the structure of the males is so similar to that of male *Bothroprosopa* and *Tonnoiriphora* that it seems inevitable that they will form a monophylum. I predict that the females, when found, will in fact have tergite 7 present.

4.6.2 *Tonnoiriphora* new genus

Triphleba (*Tonnoirina*) Schmitz 1939

(Fig. 4.4E)

Type species: *Triphleba* (*Tonnoirina*) *rufithorax* Schmitz 1939 (designated by Schmitz 1941, pg 128).

Derivation of generic name. Named after the Belgian entomologist, André Léon Tonnoir, who worked for many years in Australia and New Zealand.

When elevating this former subgenus of *Triphleba* Rondani to generic status, I was unable to use the name *Tonnoirina* Schmitz, as it is preoccupied by *Tonnoirina* Edwards (Diptera: Blephariceridae) (Schmitz, 1941). The name *Tonnoiriphora* was chosen as an acceptable alternate, retaining the tribute to Tonnoir.

Notes about synonymy. Schmitz (1939) seemed unsure of the proper placement of this genus but speculated that if it did not belong as a subgenus of *Triphleba*, as he recognized it, it probably belonged with the *Borophaga*-group of genera, as he understood it. Examination of some previously undescribed male specimens showed that this speculation was correct.

Diagnosis. Wing vein R_{2+3} present. Inner lobe of hypandrium reduced (as in *Bothroprosopa*, Fig. 4.4B), but still present. Tergite 7 present in female.

Way of life and immature stages. Unknown.

Geographical distribution. New Zealand.

Phylogenetic relationships. This genus belongs near the base of the Hypocerinae, as it retains primitive character states such as the presence of wing vein R_{2+3} and presence of inner hypandrial lobes. The male terminalia of all of the New Zealand endemic genera *Tonnoiriphora*, *Palpocrates*, *Tarsocrates* and *Bothroprosopa* are extremely similar (Figs. 4D-E); these are here placed in the *Bothroprosopa*-group of genera.

No autapotypic character states can be proposed at this time for *Tonnoiriphora*.

Number of recognized species: Three.

Material examined. unidentified ***Tonnoiriphora*** spp. 1♂, NEW ZEALAND: S. Oferiangipuku R., L. Brunner, South Island, 11.i.1978, H.Oliver, Malaise trap (BVB); 2♀, Buller, Punakaiki, 29.xii-3.i.1984, L.Masner, Malaise trap, *Nothophagus* forest

(BVB).

4.6.3 *Palpocrates* Schmitz 1939

Type species: *Palpocrates rufipalpis* Schmitz (original designation).

Derivation of generic name. This name means "strong palp" referring to the enlargement of this structure.

Diagnosis. Frons not excavated. Palpi enlarged, elongate. Wing vein R_{2+3} present.

Way of life and immature stages. Unknown.

Collecting methods. Unknown.

Geographical distribution. New Zealand.

Phylogenetic relationships. Unknown. See *Tonnoiriphora*.

Number of recognized species. Two.

Material examined. ***P. rufipalpis*** **Schmitz**, 1♂ paratype, NEW ZEALAND: Nelson, 1.xi.1923, A.Tonnoir (ZFMK).

4.6.4 *Tarsocrates* Schmitz 1939

Type species: *Tarsocrates niger* Schmitz (original designation).

Derivation of generic name. This name means "strong tarsus" referring to the enlargement of these structures.

Diagnosis. Apical tarsomeres of all legs enlarged, with enlarged claws and pulvilli. Wing vein R_{2+3} present.

Way of life and immature stages. Unknown.

Collecting methods. Unknown.

Geographical distribution. New Zealand.

Phylogenetic relationships. Unknown. See *Tonnoiriphora.*

Number of recognized species. One.

Material examined. ***T. niger*** **Schmitz**, 1♂ paratype, NEW ZEALAND: Nelson, 28.xi.1923, A.Tonnoir (ZFMK).

4.6.5 ***Bothroprosopa*** **Schmitz 1939**

(Figs. 4.4B, 4.4D)

Type species: *Bothroprosopa mirifica* Schmitz 1939 (by monotypy).

Derivation of generic name. Literally translated as "trench face", referring to the enlarged antennal cavities.

Diagnosis. Male with enormously elongate, upturned palpi, that nearly reach vertex; frons deeply excavated to receive the palpi. Wing vein R_{2+3} absent. Female tergite 7 present. Inner lobe of hypandrium reduced (Fig. 4.4B), but still present.

Way of life and immature stages. Unknown.

Geographic distribution. New Zealand.

Phylogenetic relationships. Unknown. This genus is part of the New Zealand based

Bothroprosopa-group.

Hypothesized autapotypic character states of *Bothroprosopa* include the following:

1 Palpi enormously elongate in male, with correspondingly excavated frons.

Number of recognized species: One.

Material examined. ***B. mirifica*** **Schmitz**, NEW ZEALAND: 1♂, 1♀, North Island, Coremanddra Mt., Moehau, 22-25.iv.1984, H.Oliver, Malaise trap (BVB); 20♂, 2♀, Buller, Punakaiki, 29.xii-3.i.1984, L.Masner, Malaise trap, *Nothophagus* forest (BVB); 2♂, Waikato, Ngaruawahia, Hakarimata Range, 27.xi.1983, Malaise trap, H.Oliver, *Leptospermum* bush (BVB).

4.6.6 *Hypocera* Lioy 1864

(Figs. 4.2A, 4.4C, 4.4F)

Type species: *Trineura mordellaria* Fallén 1823 (designated by Brues, 1906).

Derivation of generic name. *Hypocera* literally translated means "under wax" and may refer to the occurrence of one of the species in this genus in wasp nests.

Diagnosis. Anepisternum with long seta. Hind tibia with transverse rows of ctenidia (Fig. 4.2A).

Way of life and immature stages. The type species, *H. mordellaria*, has been reared from a wasp nest (Perris in Borgmeier, 1963) and from fungus (Colyer, 1954). In older records, such as that of Perris, the identity of the species involved is questionable, especially since a species of phorid (*Gymnoptera vitripennis* (Meigen)) formerly classified in this genus is known to be associated with wasps.

Immature stages are undescribed.

Collecting methods. These flies can be trapped in Malaise traps, yellow pan traps, pitfall traps and flight-intercept-traps early in the spring.

Geographical distribution. Europe, North America, Southeast Asia (Burma, Java, Taiwan, Thailand).

Phylogenetic relationships. This genus is the adelphotaxon of the *Borophaga*-group of genera.

The two North American species, *H. americana* and *H. ehrmanni*, do not display the character state wing vein M_1 curved, that unites most other Hypocerinae. *Hypocera rectangulata* Malloch (1912; Java), *flavipennis* (Enderlein) (1924; Taiwan, Burma), *mordellaria* (Fallěn) (1823; Europe), *semirufa* Beyer (1958; Burma), and the unidentified Japanese species that I examined, however, all have M_1 curved according to the literature. Thus, the two Nearctic species may form a monophyletic group, with a straight vein M_1 as a tentative synapotypy (reversal). The alternative view, that the Nearctic species may not belong in a genus with the other species, is disputed by the two fairly distinctive autapotypies listed above, that link them to the other world species, and by the congruence of the genitalia of the Japanese species with the two Nearctic species (Fig. 4.4F).

Hypothesized autapotypic character states of *Hypocera* include the following:

1 Anepisternum with long seta.

2 Hind tibia with transverse rows of enlarged setulae.

Number of recognized species: Six.

Material examined: ***H. americana*** **Borgmeier**, 1♂, CANADA: Ontario: Stouffville, 21-28.v.1985, B.V.Brown, Malaise pans (BVB); ***H. ehrmanni*** **Aldrich**, 1♂, CANADA: Ontario: Guelph, South Arboretum, 7-22.v.1984, yellow pan trap, deciduous forest, 1♂, 30.iv.-7.v.1985, Malaise pans at forest edge, 1♂, 11-16.v.1985, Malaise trap, wet, shrubby meadow, 1♂, 11-16.v.1985, Malaise trap, forest edge, 1♂, 24-30.v.1985, Malaise trap, forest edge, B.V.Brown (BVB); ***H. mordellaria*** **(Fallén)**, 1♂, COUNTRY?: Wendbadetal, 10.v.1946, Enns (ZFMK); ***H. semirufa***, 1 paratype ♂: BURMA: N.E. Burma, Kambaiti, 7000ft, 11.v.1934, Malaise trap (ZFMK); ***Hypocera*** **sp.1**, JAPAN: 1♂, Shikoku, Ishizuchi Mt. N.P., Tsuchigoya, 1400m, 11-18.viii.1980, S.Peck (BVB); ***Hypocera* sp. 2**, 1♀, THAILAND: 70km SW Chiang Mai, Doi Inthanon National Park, 2200m, 6-12.v.1990, B.V. Brown, Malaise trap, oak forest (BVB).

***Borophaga*-group**

Diagnosis. Supra-antennal setae absent; inner lobe of hypandrium absent.

***Borophaga*-subgroup**

Diagnosis. Epandrium expanded below cerci.

4.6.7 ***Borophaga* Enderlein 1924**

(Figs. 4.1A-F, 4.3A, 4.3C, 4.4G, 4.7A)

Type species: *Phora flavimana* Meigen 1830 (=*Phora femorata* Meigen 1830) (original designation).

Derivation of generic name. A literal translation of this name could be "city eater", apparently referring to a possible synanthropic lifestyle.

Notes about synonymy. There are problems evident with the two recognized subgenera of *Borophaga*, *Borophaga s.s.* (including all of the Nearctic species as well as the type species) and *Peromitra* Enderlein. It is clear from illustrations of male terminalia given by Schmitz (1951), and from specimens that I examined (Figs. 4.6A-D), that species of *Peromitra* belong to the lineage with *Stichillus* and not with true *Borophaga*. For instance, the male terminalia of *B.* (*Peromitra*) *carinifrons* (Schmitz, 1951, Fig. 152.2) looks exactly like those of *Stichillus* species. Also, the defining character of *Peromitra* is a modified (raised) ocellar region, which is an area also greatly modified in species of *Stichillus*. The genus *Borophaga*, as currently defined, is therefore polyphyletic. Since members of the subgenus *Peromitra* are more closely related to *Stichillus* and *Trineurocephala* than to *Borophaga s.s.*, the subgenus *Peromitra* must be given full generic status (**new status**). The affected species are the following: *P. agilis* (Meigen) (Europe), *P. carinifrons* (Zetterstedt) (Europe), *P. cephalotes* (Schmitz) (Europe), *P. erythrocera* (Meigen) (Europe), *P. eumimeta* (Beyer) (Burma), *P. incrassata* (Meigen) (Europe), *P. multisetalis* (Colyer) (USSR), and *P. subagilis* (Beyer) (Burma) (all **new combinations**). Furthermore, other species classified in the typical subgenus of *Borophaga* belong in *Peromitra*, specifically *P. amurensis* (Schmitz) (Siberia), *P. cornigera* (Beyer) (Burma), and *P. germanica* (Schmitz) (Europe) (all **new combinations**). The following species are classified in *Godavaria* new genus described below: *G. eminens* (Beyer) (Burma), *G. inflata* (Beyer) (Burma), *G. minor* (Beyer) (Burma), and *G. orientalis* (Beyer) (Burma). The generic name *Borophaga* now only applies to the following taxa: *B. clavata* (Loew) (North America), *B. femorata*

(Meigen) (Europe), *B. fuscipalpis* Schmitz (North America), *B. irregularis* (Wood) (Europe), *B. subsultans* (Linnaeus) (Holarctic Region), *B. tinctipennis* Borgmeier (North America) and *B. verticalis* Borgmeier (North America). The relationships of *B. thoracalis* Beyer (Burma) are unknown, as the species was described from female specimens only. Until the male is discovered, this species is also retained in *Borophaga*. I have not examined any specimens of *B. simia* Beyer (Africa), but it is apparently closely related to *B. rufibasis* Beyer (Africa) and *B. pachycostalis* (Borgmeier) (Neotropical Region), that are placed in a new genus *Latiborophaga* below. From the illustrations given by Borgmeier & Prado (1975), *B. insignis* Borgmeier & Prado (Neotropical Region) appears to be merely the male of *B. pachycostalis*.

Diagnosis. Apex of wing vein R_{4+5} apically swollen (Fig. 4.7A, as).

Way of life and immature stages. Unknown; previous references to the life history of *Borophaga* referred to *Peromitra incrassata*.

Collecting methods. Malaise traps seem to be the best collecting technique for members of this genus.

Geographical distribution. Holarctic Region.

Phylogenetic relationships. This genus is most closely related to *Godavaria*, *Latiborophaga*, *Abaristophora* and *Antipodiphora*, however I am able to find only one autapotypic character state in adults of *Borophaga* with respect to these other taxa, namely the characteristic swollen apex of wing vein R_{4+5}.

Hypothesized autapotypic character states of *Borophaga* include the following:

1 Apex of wing vein R_{4+5} swollen (Fig. 4.7A, as).

Number of recognized species. Nine.

Material examined: ***B. clavata*** **(Loew)**, 3♂, CANADA: Ontario: Guelph, South Arboretum, 24-30.v., 27.ix.-8.x.1985, B.V.Brown, Malaise trap, deciduous forest, wet shrubby meadow (BVB), 2♂, Ontario: Stouffville, 5-12, 12-26.v.1985, B.V.Brown, Malaise trap (BVB); ***B. femorata*** **(Meigen)**, 1♂, NETHERLANDS: Valkenburg, H.Schmitz (ZFMK); ***B. fuscipalpis*** **Schmitz**, 2♂, CANADA: Ontario: Guelph, South Arboretum, 22-30.v, 16.ix-1.x.1985, B.V.Brown, Malaise trap, deciduous forest (BVB), ***B. irregularis*** **(Wood)**, 1♂, BELGIUM: Grotte de Tridaine, 4.ix.1935, R.Leruth (ZFMK); ***B. subsultans*** **(Linnaeus)**, many ♂ and ♀ specimens, collected in Malaise and pan traps from May to September at the following localities: CANADA: Alberta: Edmonton, Opal; New Brunswick: St. Andrew's; Ontario: Algonquin Provincial Park, Footes Bay, Guelph, Pukaskwa National Park, Stouffville; ***B. thoracalis*** **Beyer**, 1♀, BURMA: Kambaiti, vi.1934, Malaise (ZFMK); ***B. tinctipennis*** **Borgmeier**, 2♀, CANADA: Ontario: Guelph, 27.ix-16.x.1985, B.V.Brown, Malaise trap, deciduous forest, wet shrubby meadow (BVB); ***B. verticalis*** **Borgmeier**, 1♂, 1♀, UNITED STATES: Arizona: Cochise Co., near Portal, S.W.R.S., 27.vii, 25.viii.1965, V.Roth, Malaise trap (BVB), 4♂, 1♀, Coconino Co., 20 miles N. Flagstaff, Bonito Park, 5-8.viii.1984, 7000', B.V.Brown, Malaise trap, ponderosa pine/meadow (BVB).

4.6.8 *Godavaria* new genus

(Figs. 4.5A-D, 4.7B)

Type species: *Godavaria setulosa* new species (present designation)

Derivation of generic name. Named for the locality where one species of this genus was collected- Godavari, Nepal.

Notes about synonymy. When he proposed the new species *B. eminens*, *B. inflata*, *B. minor* and *B. orientalis*, Beyer extended the defintion of the genus *Borophaga* to include species with wing vein R_{2+3} present. This extension is untenable when these species lack the synapotypy proposed to link species of *Borophaga* (apically expanded wing vein R_{4+5}; see above) and when the presence of R_{2+3} is considered a derived state within the *Borophaga*-subgroup lineage.

Diagnosis. Borophaga- group, but flagellomere 1 not elongate and pointed; wing vein R_{2+3} present (Fig. 4.7B); wing vein R_{4+5} not apically swollen.

Way of life, immature stages and collecting methods. Unknown. The reduced mouthparts suggest that the males of this genus do not feed and probably have a short adult life. According to Fleming (1977) the general habitat at Godavari, Nepal at 6000' (= 1846m) is oak (*Quercus leuchotricophora*) forest. The habitat in Thailand, where *G. minor* was collected, was also oak forest.

Geographical distribution. Burma, Nepal, Thailand.

Phylogenetic relationships. This genus belongs in the *Borophaga-* group of genera, but its exact adelphotaxon is unknown. The proboscis of the female is more elongate than that of female *Borophaga*, but in most species is shorter than that of female *Abaristophora* and *Antipodiphora*. Since a moderately elongate proboscis is also found in females of outgroup taxa such as *Hypocera*, *Tonnoiriphora* and *Bothroprosopa*, this character state cannot be used to justify an adelphotaxon relationship between *Godavaria* and *Abaristophora* + *Antipodiphora*.

The presence of wing vein R2+3 must be considered a reversal, as adults of *Bothroprosopa*, *Hypocera*, almost all other *Stichillus*-subgroup (except some *Peromitra*) and *Borophaga*-subgroup (except some *Borophaga*) genera lack this structure.

Hypothesized autapotypic character states of *Godavaria* include the following:

1 Wing vein R_{2+3} present (Fig. 4.7B).

Number of recognized species. Five, including one new species described below.

Species recognition. Males can be identified using the following key. Females were not keyed because characters to separate females of *G. minor* and *G. orientalis* will only be found after a species level revision of this group.

Key to males of *Godavaria*

1 Right side of hypandrium with long, setulose process (Fig. 4.5B) ..... *G. setulosa* new species (Nepal)

1' Right side of hypandrium with short process (Fig. 4.5D) or no process (Fig. 4.5C) 2

2 Right side of hypandrium with short process, right side of epandrium broad, posteriorly-directed (Fig. 4.5D) ..... *G. orientalis* (Beyer) (Burma)

2' Right side of hypandrium without process, right side of epandrium narrower, posteroventrally directed (Fig. 4.5C) ..... *G. minor* (Beyer) (Burma, Thailand)

G. eminens (Beyer) new combination

Borophaga (Borophaga) eminens Beyer 1958

Species recognition. Characters to separate *G. eminens* from *G. inflata* are given by Beyer (1958). This species, and *G. inflata*, are known only from female specimens. Opportunity to collect males of *G. eminens* or *G. inflata* at the type locality in Myanmar (Burma) is unlikely because of the present political situation within that country.

Material examined. 1♀ paratype, BURMA: Kambaiti, 2000m, 9.vi.1934, *Malaise* (ZFMK).

G. inflata (Beyer) new combination

Borophaga (Borophaga) inflata Beyer 1958

Species recognition. See *G. eminens*.

Material examined. 1♀ paratype, BURMA: Kambaiti, 2000m, 4.vi.1934, *Malaise* (ZFMK).

G. minor (Beyer) new combination

Borophaga (Borophaga) minor Beyer 1958

(Figs. 4.5C, 4.7B)

Species recognition. This species is distinguished from *G. setulosa* by the absence of a posterior hypandrial process. Also, the ventral hypandrial processes of *G. setulosa* project below the level of the rest of the hypandrium, whereas in *G. minor* these processes are level with the rest of the hypandrium. The presence of a large seta on the left side of the epandrium may be diagnostic for this species, but it is possible this seta was originally present on the type specimen of *G. setulosa* as well. This seta could have been removed accidently at some point, as there is an empty setal socket on the epandrium.

Material examined. BURMA: 1♂, 1♀ paratype, Kambaiti, 2000m, [date?].1934, *Malaise* (ZFMK); 2♂, THAILAND: 70km SW Chiang Mai, Doi Inthanon National Park, 2200m, 6-12.v.1990, B.V.Brown, Malaise trap, oak forest (CNC).

G. orientalis (Beyer) new combination

Borophaga (Borophaga) orientalis Beyer 1958

(Fig. 4.5D)

Derivation of specific epithet. Presumably, this species was named for the Oriental Region.

Species recognition. The males of this species can be separated using the key, above.

Material examined. 1♂, 1♀ paratype, BURMA: Kambaiti, 2000m, *Malaise* (ZFMK).

G. setulosa new species

(Figs. 4.5A-B)

Derivation of specific epithet. This name refers to the setulose hypandrial process.

Description. Body length 1.8mm (male)- 2.5mm (female). Head and abdomen dark brown, thorax ferruginous, legs yellowish brown, except mid-coxa darker. Supra-antennal setae absent. Frontal setae 4-4-4. Flagellomere 1 ferruginous, arista dorsal. Mouthparts of male reduced, labellae thin and probably non-functional; those of female form elongate proboscis. Scutellum with 2 pairs of setae, the anterior pair much shorter and thinner than posterior pair. Fore-tibia with large anterodorsal seta on basal third; mid-tibia with large anterodorsal and posterodorsal seta basally and row of three small, sub-apical setae; hind-tibia with pair of dorsal, longitudinal rows of enlarged setulae and apical anterodorsal seta. Wing with mean costal ratio (n=2) 0.57, range 0.57-0.58; mean costal sector ratio 4.7: 4.4: 1, range 4.7-4.8: 4.1-4.7: 1; vein R_{2+3} present. Halter stem yellow, knob dark brown. Abdomen of male ventrally with long, scattered setae; setae on female abdomen short. Female abdominal tergites sucessively smaller, tergite 6 equilateral triangle-shaped. Male terminalia with ventral process extended ventrally below level of rest of hypandrium; right side of hypandrium with thin, elongate, setulose process (Figs. 4.5A-B). Right side of epandrium with truncate process, with one large seta, many smaller setae and four extremely small setae. Aedeagus extremely complex, as in other *Borophaga*- group genera. Female terminalia internally with T-shaped sclerite; tergite 8 small; anal segment with dark lateral sclerites.

Material examined. HOLOTYPE ♂, NEPAL: 13 km S Kathmandu, Godavari, 6000', 17.vii.1967, Malaise trap, Canadian Nepal Expedition (CNC).

PARATYPES, 2♀, same data as holotype (BVB, CNC).

4.6.9 *Latiborophaga* new genus

(Figs. 4.3D, 4.5E, 4.7C-F)

Type species: *Borophaga rufibasis* Beyer 1959 (present designation)

Derivation of generic name. Named for the widened costal vein of the wing, plus the name *Borophaga*, the genus in which these species originally were described.

Notes about synonymy. Adults of four distinctive species of *Borophaga* from the Neotropical and Afrotropical Region have the costa enlarged in sector 1. These species do not have the swollen apex of wing vein R_{4+5} that characterizes members of the genus *Borophaga*; therefore, they are placed in a new genus, diagnosed below. The affected taxa are *L. insignis* (Borgmeier & Prado), *L. pachycostalis* (Borgmeier), *L. rufibasis* (Beyer), and *L. simia* (Beyer), all **new combinations**.

As stated above, *L. insignis*, known only from a single male specimen is probably conspecific with *L. pachycostalis*, known only from female specimens. The differences in wing venation cited by Borgmeier & Prado (1975) as the main characters to separate the two species represent normal sexual dimorphism in this genus (compare Figs. 4.7C with 4.7D, 4.7E with 4.7F).

Diagnosis. *Borophaga*- group, but flagellomere 1 not elongate; costa of female markedly thickened (4.7D,F), wing vein R_{2+3} absent, vein R_{4+5} not apically enlarged; wing vein R_s deflected at midlength; hypandrium with dense setulae (Fig. 4.3D, hs).

Way of life, immature stages and collecting methods. Unknown.

Geographical distribution. Neotropical and Afrotropical Regions.

Phylogenetic relationships. Unknown. The male terminalia resemble those of species of *Godavaria*, but no synapotypic character states were found to link these two genera.

Hypothesized autapotypic character states of *Latiborophaga* include the following:

1 Costa swollen in female (Figs. 4.7D, cs, 4.7F, cs).

2 Wing vein R_s deflected posteriorly (Figs. 4.7C, d, 4.7F, d).

Number of recognized species. Four.

Material examined. I was unable to identify the specimens from South Africa without seeing specimens of *A. simia* for comparison, as the description given by Beyer (1965) for this species is substandard. ***L. pachycostalis* Borgmeier**, 1♂, 1♀, VENEZUELA: Lara, Yacambú, 1200m, 7.v.1981, H. Townes, Malaise trap (BVB); ***L. rufibasis* (Beyer)**, 1♀ paratype, TANZANIA: Msingi, 1-19.v.1952 (ZFMK), ***Latiborophaga* sp.**, 5♂, 5♀, SOUTH AFRICA: Natal, 75km WSW Estcourt, Cathedral Peaks For. Sta., 7-31.xii.1979, S.&J.Peck (CNC, BVB).

4.6.10 *Antipodiphora* Schmitz 1939

(Fig. 4.5F)

Type species: *Abaristophora (Antipodiphora) tonnoiri* Schmitz 1939 (by original designation).

Derivation of generic name. Named after the Antipodes Islands (New Zealand).

Diagnosis. Male flagellomere 1 elongate, pointed, arista present (Schmitz, 1939, Fig. 2). Hypandrium with dense setulae.

Way of life and immature stages. Unknown.

Geographical distribution. New Zealand, but previously more widespread, as shown by fossil specimens in Dominican amber.

Phylogenetic relationships. This genus resembles *Abaristophora* in all examined characters, as discussed below. It is probably not a valid genus.

Autapotypic character states cannot be proposed for *Antipodiphora* at this time, since all known character states are primitive relative to character states found in species of *Abaristophora*. The two genera need revision.

Number of recognized species. Six.

Material examined: ***Antipodiphora* sp.**, 2♂, NEW ZEALAND: BR, Punakaiki, 29.xii-

3.i.1984, L.Masner, Malaise trap, *Nothophagus* forest (BVB); WO, Raglan, Mt.Karioi, 17-24.viii.1983, H.Oliver, Malaise trap near stream (BVB); 3♂, DOMINICAN REPUBLIC: La Toca Mine, in amber (BVB).

4.6.11 ***Abaristophora*** **Schmitz 1927**

(Fig. 4.5G)

Type species: *Abaristophora arctophila* Schmitz 1927 (by monotypy)

Derivation of generic name. This name refers to the lack of an arista in the antennae of adult males.

Diagnosis. Frons of female produced between antennae. Proboscis of female elongate, geniculate. Male with elongate flagellomere 1, arista absent.

Way of life and immature stages. Unknown.

Collecting methods. These flies have been collected in Malaise traps.

Geographical distribution. All species are known from the Holarctic Region.

Phylogenetic relationships. The adelphotaxon of *Abaristophora* is *Antipodiphora*.

The female of this genus, previously unknown, was diagnosed from several specimens from the western United States (Brown, 1988). The discovery of this female calls into question the validity of *Antipodiphora* Schmitz (1939), a genus that is known only from extant species in New Zealand and a fossil species from Dominican amber. Originally, Schmitz proposed that the genus *Abaristophora* contained two subgenera, namely *Abaristophora s.s.* and *Antipodiphora*. The typical subgenus, *Abaristophora s.s.*, for which there were only male specimens known, was characterized by the lack of an arista and the extreme sigmoidal curvature of wing vein CuA_1. The corresponding character states for *Antipodiphora*-- arista present and CuA_1 normal-- are obviously plesiotypic, and do not constitute justification of a monophyletic taxon. The two character states that were previously considered to be restricted to female *Antipodiphora*, namely a geniculate proboscis and an extended frons, occur in *Abaristophora* as well. Thus, Borgmeier (1963, p.76) was unjustified to giving *Antipodiphora* generic ranking. I prefer not to synonymize the two names, however, until the relationships between the New Zealand species have been determined.

Hypothesized autapotypic character states of *Abaristophora* include the following:

1 — Arista absent from male antenna.

Number of recognized species. Three.

Material examined. ***A. diversipennis* Borgmeier**, UNITED STATES: California. 1♂, Modoc Co., Cedar Pass Campground, 11.viii.1967, 1800m, P.H.Arnaud, Jr (BVB); 1♂, 1♀, Siskiyou Co., McBride Springs, 8.viii.1967, 1524m, P.H.Arnaud, Jr (CAS). Idaho. 1♀, Franklin Co., Cub River Canyon, 20.vii.-7.viii.1985; 2♂, 7.viii.-17.ix.1985, Malaise trap, W.J.Hanson (USU).

***Stichillus*-subgroup**

Diagnosis. Apical foretarsomere enlarged (Figs. 4.2D-F). Male with sternites on abdominal segments 5 and 6. Aedeagus tube-shaped (Fig. 4.6D).

4.6.12 ***Peromitra* Enderlein 1924 new status**

(Figs. 4.2B, 4.3B, 4.3E, 4.6A-D)

Type species: *Phora incrassata* Meigen 1830 (by original designation).

Derivation of generic name. A literal translation of *Peromitra* is "maimed turban", apparently referring to the modified, elevated ocellar region.

Diagnosis. Anterior ocellus oval (Fig. 4.3E). Ocellar region raised. Male abdominal segment 6 with paired or single sternite.

Way of life and immature stages. Morris (1922) reported that *P. incrassata* is an endoparasite of larval *Bibio marci* (Linnaeus) (Diptera: Bibionidae), and provided a description of the immature stages. Packard (1868) stated that this same species was an internal parasitoid of larval *Apis mellifera* (Hymenoptera: Apidae), but this record is highly suspect (R.H.L. Disney, personal communication). A second species, *P. germanica*, is a parasitoid of another bibionid, *Penthretia holosericea* (Gemesi & Disney, in press), and this way of life may be characteristic of *Peromitra* species.

Geographical distribution. Europe, Russia, Burma, Thailand.

Phylogenetic relationships. As noted above (Notes about synonymy for *Borophaga*) this former subgenus must be treated as a full genus. It shares several synapotypies with its sister-taxa, *Stichillus* and *Trineurocephala*, such as presence of sternite 6, and form of the aedeagus. While it is obvious that these species do not belong with *Borophaga*, it is less clear whether they represent a genus distinct from *Stichillus*. They lack the synapotypy of widely spaced ocelli, found in *Stichillus*, but have an elevated ocellar region, found to some extent in both of these genera. Thus, these species may be part of the stem-group of *Stichillus*, and may be a paraphyletic assemblage. The major defining character for this genus (formerly in contrast to other species classified in *Borophaga*) is the presence of an elevated ocellar region. Some species examined, however, specifically *P. agilis* and *P. eumimera*, have only a slightly elevated ocellar region. Schmitz (1929, 1951) considered *P. agilis* to be a perfect intermediate between the two subgenera of *Borophaga*, but this view cannot be maintained in light of our current knowledge about the phylogeny of the Hypocerinae. A slightly raised ocellar region must be part of the groundplan of the *Stichillus*-subgroup, and thus cannot be used as a character to justify the genus *Peromitra* alone. I propose that the presence of an oval, rather than round, lower ocellus is a synapotypy for most species of this genus (Fig. 4.3E). The degree of this modification is various, and seems to increase with increasing elevation of the ocellar region. Some species do not have this character state, but otherwise resemble species of *Peromitra* with enlarged lower ocelli; the correct placement of these species will only accomplished when this genus is fully revised. Species of the genus *Stichillus* have round lower ocelli.

Hypothesized autapotypic character states of *Peromitra* include the following:

1 Lower ocellus oval-shaped (Fig. 4.3E)

Number of recognized species. Eleven.

Material examined. ***P. agilis*** **(Meigen)**, POLAND: 1♂, Silesia, Duda (ZFMK), COUNTRY?: 1♂, Ziliebake, 12.vii.1939, M. Goetghabuer (ZFMK); ***P. amurensis*** **(Schmitz)**, 1♂, USSR: Amur Fl., Nikolajewsk., 1.ix.1917, Y.Wuorentaus (ZFMK); ***P. carinifrons*** **(Zetterstedt)**, FINLAND: 1♂, Tvärminne Biol. Stn, 6-10.viii.1969, G.C. and D.M. Wood (CNC); ***P. cornigera*** **(Beyer)**, 1♂, BURMA: Kambaiti, 2000m, 4.vi.1934, *Malaise* (ZFMK); ***P. erythrocera* (Meigen)**, GERMANY: 1♂, Berlin, 18.ix.190?, Bernuki (ZFMK), 1♂, Frankfurt, M.P. Riedel (ZFMK), SWITZERLAND: **Canton de Vaud**: 3♂, Cudrefin, 435m, 5.ix.1972, P.H. Arnaud, Jr (BVB); ***P. eumimeta*** (Beyer), BURMA: 1♂, Kambaiti, 2000m, 14.v.1934, *Malaise* (ZFMK); ***P. germanica* (Schmitz)**, 1♂, AUSTRIA: Bad Véllach, 13.vii.1937, Oedbg (ZFMK); ***P. incrassata*** (Meigen), GERMANY: Berlin, 16.viii.1909 (ZFMK), SWITZERLAND: **Canton de Vaud**: 1♂, Cudrefin, 435m, 5.ix.1972, P.H. Arnaud, Jr (BVB), UNITED KINGDOM: **Norfolk**: 1♂, Thetford, 18.viii.1943, G.E. Shewell (CNC), **Suffolk**: 1♂, Newmarket, 19.viii.1943, G.E. Shewell (CNC), **Wiltshire**: 1♀, Salisbury, 19.viii.1954, J.R. Vockeroth (CNC), (county?) 1♂, New Forest, 24.viii.1907, J.J.F.X. King (ZFMK); ***P. subagilis* (Beyer)**, BURMA: 1♂, Kambaiti, 2000m, 4.vi.1934, *Malaise* (ZFMK); ***Peromitra* sp.1**, THAILAND: 3♂, 70km SW Chiang Mai, Doi Inthanon National Park, 1260m, 31.i.-7.ii.1989, T.W.Thormin, Malaise trap (BVB).

4.6.13 *Stichillus* **Enderlein 1924**

(Figs. 4.2C-F, 4.3F, 4.6E)

Type species: *Stichillus acutivertex* Enderlein 1924 = *Stichillus insperatus* (Brues) 1911 (by original designation)

Derivation of generic name. Presumably from the Greek word *stichos*, meaning line or row, refering to the ocelli, that Enderlein (1924) stated lie in almost a straight line.

Diagnosis. Ocellar region raised, sharply demarcated from rest of frons by curved anterior margin, posterior ocelli close to eye margin (Fig. 4.3F).

Way of life and immature stages. The type specimens of *S. acutivertex* had the following data attached (translated from German): "Collected between two leaves with a bee (parasite?)" (Enderlein, 1924). I know of no other life history data.

Collecting methods. These flies are encountered infrequently, usually in Malaise trap residues.

Geographic distribution. Worldwide, except Australia and New Zealand, mostly in tropical or subtropical regions.

Phylogenetic relationships. The most closely related genera to *Stichillus* are *Trineurocephala* and *Peromitra*. The large number of synapotypies shared by these genera raise suspicions, however, that some of these groups may be paraphyletic with respect to one another. A phylogenetic revision of all of these groups must be performed to properly deduce their relationships.

Hypothesized autapotypic character states of *Stichillus* include the following:

1 Lateral ocelli widely spaced, close to margin of eye (Fig. 4.3F).

Number of recognized species. Twenty-four.

Material examined: ***S. latipes* Borgmeier**, 2♂, ECUADOR: Napo, 5km N. El Chaco, 15.ii.1983, M. Sharkey, Malaise trap (BVB); ***S. planipes* Borgmeier**, 1♂, UNITED STATES: Arizona, Cochise Co., near Portal, S.W.R.S., 17.viii.1984, B.V.Brown, in forest near stream (BVB), 1♂, 9♀, Arizona, Cochise Co., 12.5km S.Sierra Vista, Ramsey Canyon, 13.vii-23.vii, 28.vii.-2.viii.1986, B.V.Brown, Malaise trap, 1700m, oak/pine/juniper forest (BVB); ***S. venustus* Borgmeier**, 1♂, ECUADOR: Napo, Tena, 22-27.v.1987, 500m, B.V.Brown and L.D.Coote, Malaise trap, second growth forest (BVB); 1♂ ECUADOR: Pichincha, 17km E. Santo Domingo, above Tinalandia, 9-13.v.1989, 1150m, B.V.Brown and L.D.Coote, Malaise trap, montane forest (BVB); ***Stichillus* sp. 1**, 2♂, NEPAL: Katmandu, Godavari, 5000', 29.vii, 16.viii. 1967, Canadian Nepal Expedition (CNC), 1♂, NEPAL: Katmandu, Pulchauki, 6600', 26.vii.1967, Malaise trap, Canadian Nepal Expedition (CNC); ***Stichillus* sp. 2**, PAPUA NEW GUINEA: Wau, 1.vii.1974, 400', ex. dung trap, S.Peck (CNC).

4.6.13 *Trineurocephala* Schmitz 1923

(Fig. 4.6F)

Type species: *Hypocera angustifrons* Enderlein 1912 (original designation).

Derivation of generic name. Named for the similarity of the head structure in this genus to that in *Trineura* Meigen (= *Phora* Latreille) (Schmitz, 1923).

Diagnosis. Frons of male extremely narrow, eye correspondingly large.

Description. Pair of sternites present on abdominal segments 4-6 in male; sternites of segment 6 small.

Way of life and immature stages. Unknown. These flies are infrequently collected, possibly because they are largely aerial swarmers (as suggested by the enlarged eyes), rarely descending to ground level where most entomological sampling takes place. Perhaps canopy fogging samples will yield more specimens.

Geographical distribution. Neotropical Region (Brazil, Costa Rica, Mexico).

Phylogenetic relationships. As noted above (Phylogenetic relationships for *Stichillus*) this genus is very similar to *Stichillus*, differing mainly by the narrow frons of males and the apparently unmodified ocellar region. A narrow frons also occurs in one male *Burmophora* species, in *Postoptica* Disney and in all male *Phora*, and is associated with enlarged eyes used in male aerial swarming behavior (McAlpine & Munroe, 1968), as noted for males of *Phora* and *Burmophora* by Gotô (1983, 1984).

Hypothesized autapotypic character states of *Trineurocephala* include the following:

1 Enlarged eye and narrow frons.

Number of recognized species. Three.

Material examined: Possibly *T. pubescens* (type collected in Brazil). This specimen keyed to *T. pubescens* in the key of Borgmeier and Prado (1975), but as there are likely to be undescribed species in this genus, and the type specimen was not checked, identification can only be tentative. 1♂, MEXICO: **Chiapas**, Palenque, 10.ix.1974, W.Hanson & G.Bohart (BVB).

Hypocerinae *incertae sedis*

The following genus from New Zealand has wing vein R2+3 present, and hind tibia without dorsal rows of enlarged setulae. I saw no specimens of this taxon.

4.6.15 *Ceratoplatus* Schmitz 1939

Type species: *Ceratoplatus fullerae* Schmitz (original designation).

4.7 Evolution of the male terminalia in the Hypocerinae

Many of the hypothesized character states used to justify the phylogenetic conclusions of this paper are found in the male terminalia; therefore, I offer the following discussion of the evolution of these structures.

The male terminalia of the relatively most primitive member of this group, *Burmophora*, must be close to the groundpattern states for the entire family Phoridae. A particularly primitive feature is the condition of the surstyli, that remain separate from the epandrium. The hypandrium has small, ventrally directed processes, and large inner hypandrial lobes.

The next stage of development is shown by the males of *Tonnoiriphora* and *Bothroprosopa*, which have extremely similar terminalia (Figs. 4.4D-E). Like all of the following hypocerines, males of these two genera either have lost the surstyli, or have had them fused to the epandrium such that they are undetectable. The inner lobe of the hypandrium has become greatly reduced, especially on the left side, whereas a small remnant remains on the right side (Fig. 4.4B). The hypandrial processes, that are relatively much larger than those of male *Burmophora*, become the functional terminal portions of the hypandrium. The hypandrium of males of both *Tonnoiriphora* and *Bothroprosopa* are densely setulose, unlike those of male *Burmophora*, that are bare.

The hypandria of males of the genus *Hypocera* are densely setulose, like those of *Tonnoiriphora* and *Bothroprosopa*, and retain a remnant of the right inner lobe (Fig. 4.4C), but they have also the distinctive area of thin cuticle that bears a large number of flat, rounded spinuli (Figs 4.1D-E). The function of these spinuli is unknown, but they may be sexually selected structures, used by males to induce females to use their sperm (Eberhard, 1985).

The males of some *Borophaga*-group genera lack dense setulae on the hypandrium, with only one or a few setulae present (for example Fig. 4.1C). Dense setulae are present on the hypandria of males of *Antipodiphora*, *Godavaria*, and *Latiborophaga* (Fig. 4.3D), but absent from males of *Stichillus*-subgroup genera, *Abaristophora* and *Borophaga*. Apparently they were lost at least three times: once in the *Abaristophora*-series, once in *Borophaga*, and once in the *Stichillus*-subgroup. Because of the high level of homoplasy, this character state was not used in the phylogenetic analysis. Males of *Borophaga*-group genera also have the right inner hypandrial lobe more reduced than in preceeding taxa. Otherwise, as a group their terminalia are similar to those of *Hypocera*, with the following exceptions.

The males of the *Borophaga*-subgroup have the subcercal portion of the epandrium expanded, a character state of unknown significance (Fig. 4.3C). Males of *Abaristophora diversipennis* have extremely long anteroventral processes, a character state not shared by males of other *Borophaga*-subgroup taxa (Fig. 4.5G).

Within the *Stichillus*-subgroup, the male aedeagus has a distinctive form, being an elongate, relatively simple tube (Fig. 4.6D). Males of some species have vestiges of some of the original aedeagal structures, such as the basiphallus ring, still visible, whereas the aedeagus of other species are little more than hollow tubes. Again, the function of this structure is unknown, and should be investigated relative to structure of the female terminalia.

4.8 Suggestions for future work

The phylogeny of the Hypocerinae is one of the best supported hypotheses of relationships within the Phoridae, but further work is necessary. The relationships among the genera of the *Borophaga*-subgroup and among the genera of the *Stichillus*-subgroup are unknown, and the limits of some genera need to be verified. These relationships will become apparent only after the groups in question have undergone species level revisions. Also, more work is needed on the monophyly of the genus *Tonnoiriphora* and other New Zealand hypocerines, to determine if they are in fact valid genera. In spite of these small problems, however, this subfamily remains a well understood taxon relative to other groups of Phoridae.

4.9 Acknowledgements

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Table 4.1. Distribution of plesiotypic and synapotypic character states in subfamily Hypocerinae. 0 - plesiotypic, 1 - synapotypic, stage 1, 2 - synapotypic, stage 2, ? - equivocal or unknown.

Characters	12345678901234567
Taxa	
Burmophora	00000000000000000
Tonnoiriphora	11110000?00000000
Palpocrates	111?0000000000000
Tarsocrates	111?0000000000000
Bothroprosopa	11111000000000000
Hypocera	11101111110000000
Borophaga	12101111111100000
Godavaria	12100111111100000
Latiborophaga	12101111111100000
Antipodiphora	12101111111111000
Abaristophora	12101111111111000
Peromitra	12101111111000111
Stichillus	12101111111000111
Trineurocephala	12101111001000111

Fig. 4.1. A-F. *Borophaga subsultans* (Linnaeus), male. A, frons; B, vertex; C, terminalia, left side; D, flat spinuli of hypandrium; E, flat spinuli of hypandrium; F, hind tibia, dorsal. Abbreviations: hp - hypandrial process, li - lower interfrontal setae, r - ridge, sl - spinulose lobe, ui - upper interfrontal setae

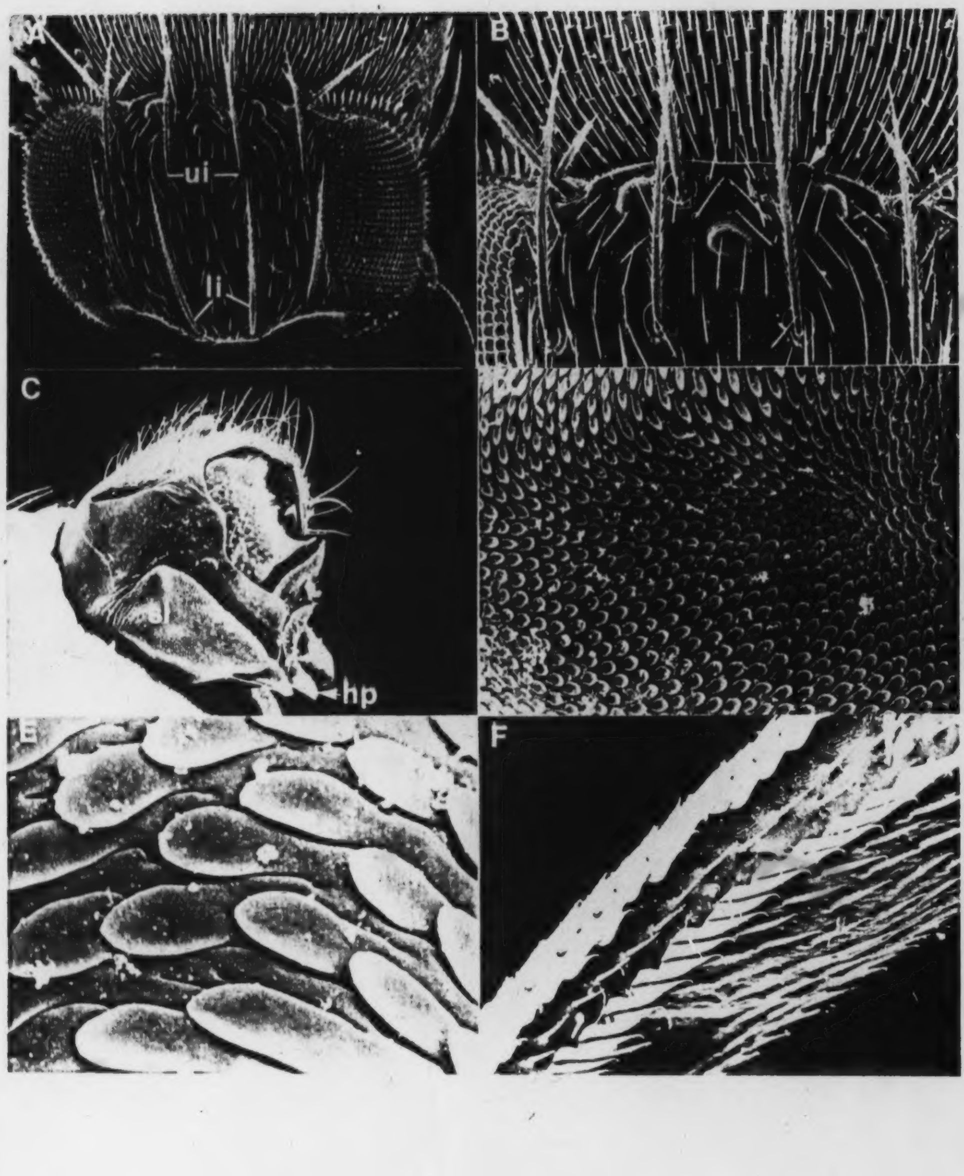

A
ui
li
B
C
hp
E
F

Fig. 4.2. A-C. hind tibiae, dorsal. A, *Hypocera ehrmanni* Borgmeier; B, *Peromitra incrassata* (Meigen); C, *Stichillus* sp.; D-F. *Stichillus* spp., apical foretarsomeres. Abbreviations: at - apical tarsomere.

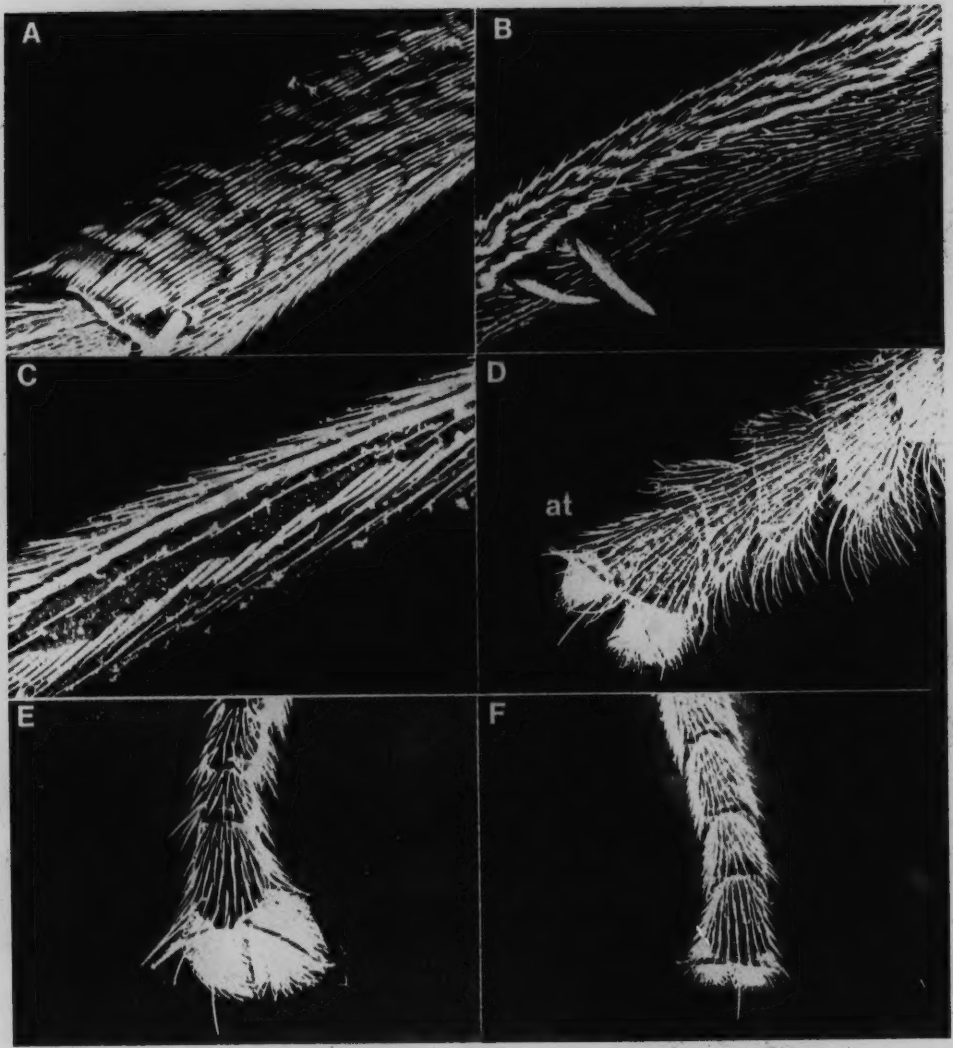

A
B
C
D
at
E
F

Fig. 4.3. A, *Borophaga subsultans* (Linnaeus), apical foretarsomeres; B, *Peromitra incrassata* (Meigen), thorax, lateral; C, *B. subsultans*, male terminalia, posterior; D, *Latiborophaga* sp., male terminalia, left lateral; E, *P. incrassata*, upper frons, frontal; F, *Stichillus* sp., vertex, dorsal. Abbreviations: ao - anterior ocellus, as - anepisternal setulae, at - apical tarsomere, es - expanded subcercal area of epandrium, hs - hypandrial setulae, ol - ocellar lobes.

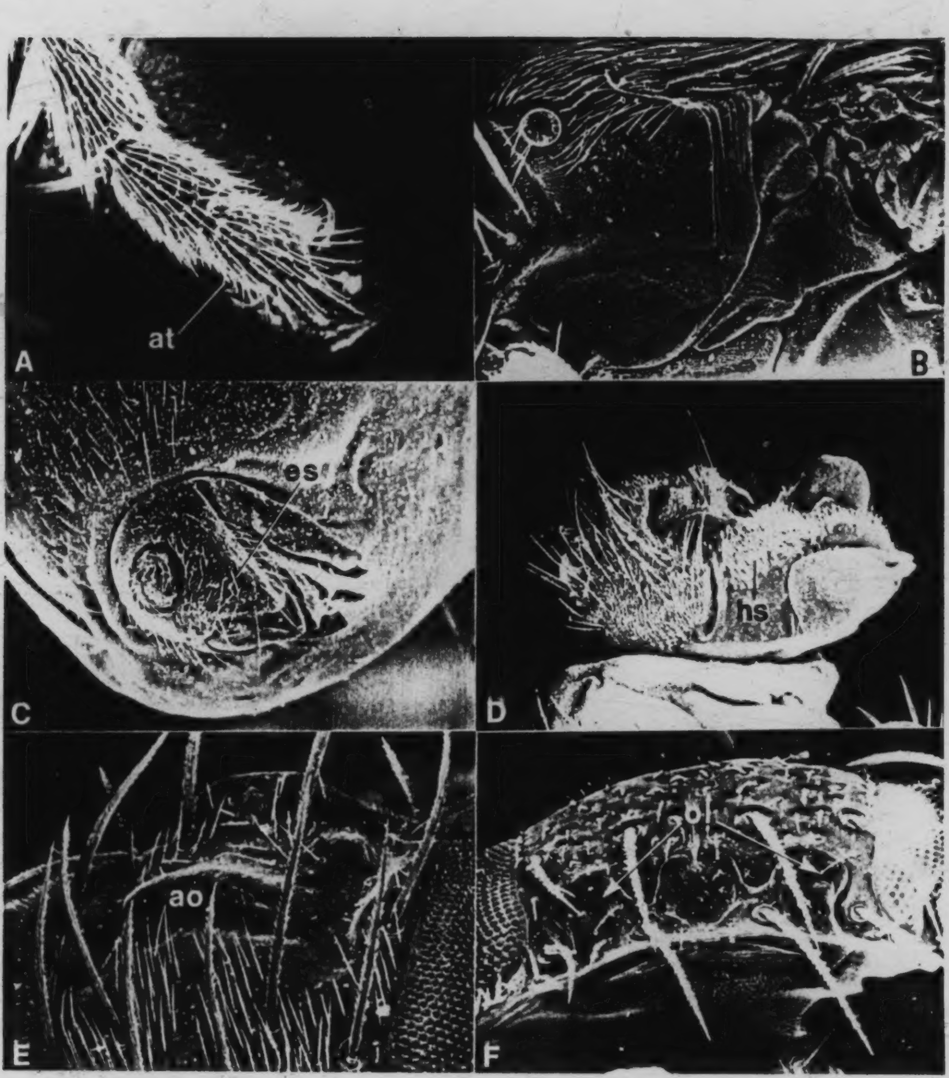

at
A
B
es
C
hs
D
ao
E
ol
F

Fig. 4.4. A-C, hypandria, ventral. A, *Burmophora comans* Beyer; B, *Bothroprosopa mirifica* Schmitz; C, *Hypocera ehrmanni* Borgmeier; D-G, male terminalia, left lateral. D, *Bothroprosopa mirifica*; E, *Tonnoiriphora* sp.; F, *Hypocera ehrmanni*; G, *Borophaga subsultans* (Linnaeus). Scale bar = 0.1mm, all figures to same scale. Abbreviations: i - inner hypandrial lobe, o - outer hypandrial lobe.

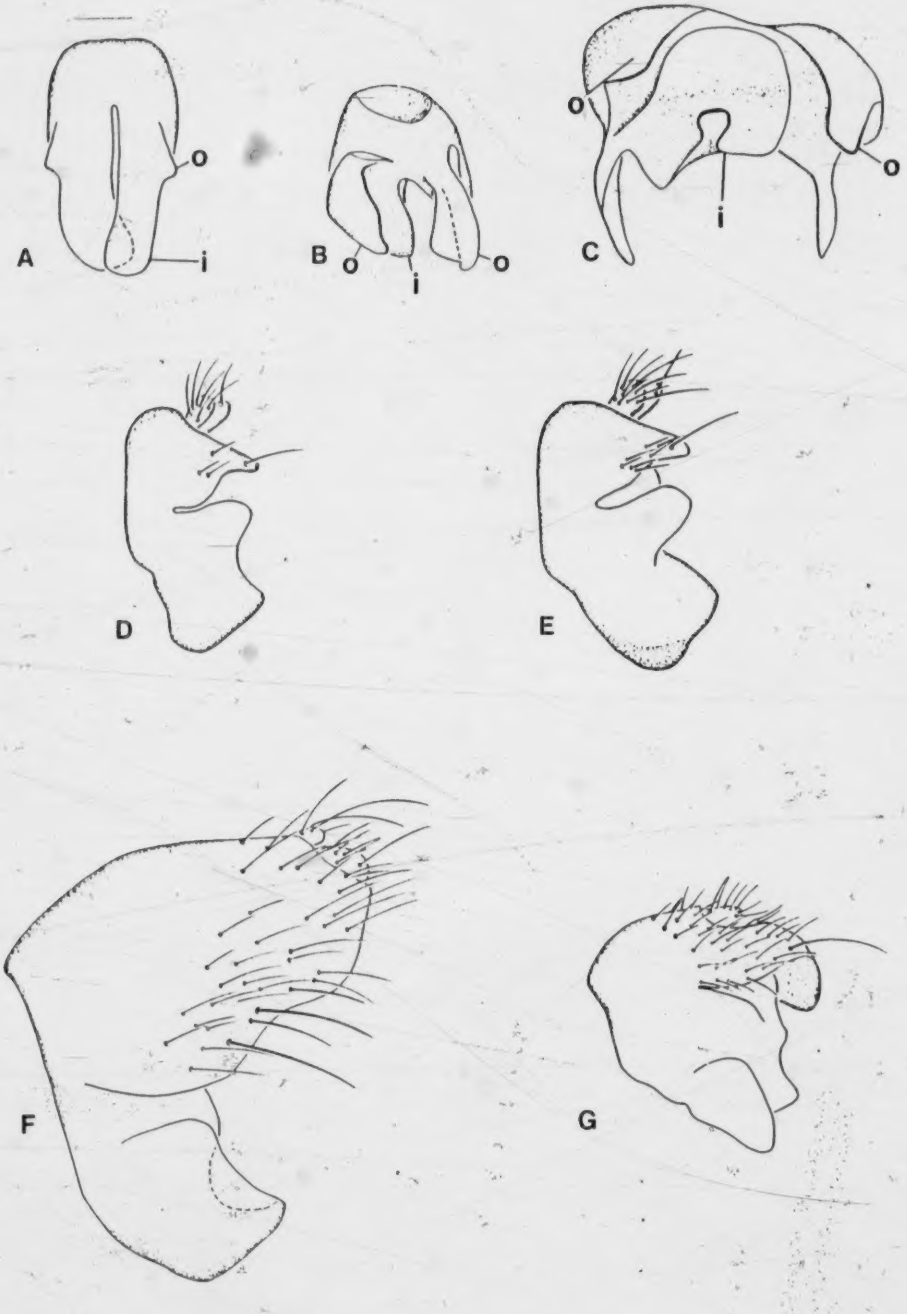

o
A
i
B
o
i
o
o
C
i
o
D
E
F
G

Fig. 4.5. A-G. Male terminalia. A-B. *Godavaria setosa* spec. n. A, left lateral; B, right lateral; C, *G. minor* (Beyer), right lateral; D, *G. orientalis* (Beyer), right lateral; E, *Latiborophaga*, left lateral; F, *Antipodiphora* sp., left lateral; G, *Abaristophora* sp., left lateral. Scale bar = 0.1mm, all figures to same scale.

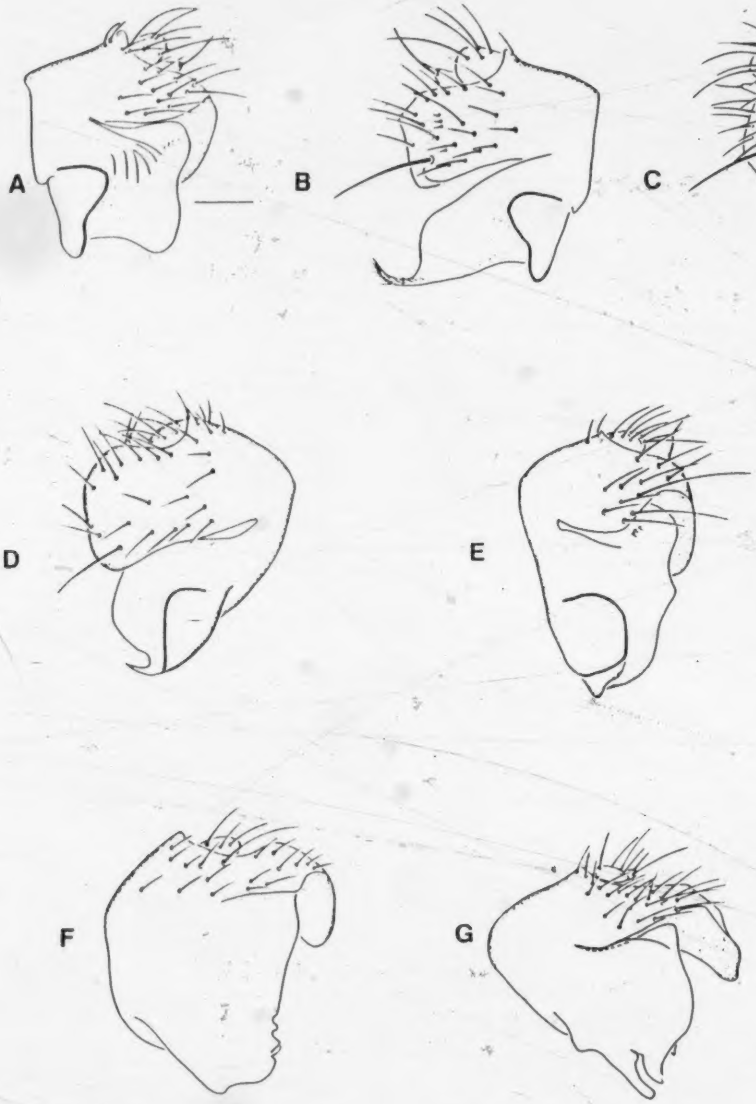

A
B
C
D
E
F
G

Fig. 4.6. A-F. Male terminalia, left lateral. A, *Peromitra incrassata* (Meigen); B, *P. erythrocera* (Meigen); C, *P. eumimeta* (Beyer); D, *Peromitra* sp. 1; E, *Stichillus* sp.; F, *Trineurocephala pubescens* Borgmeier & Schmitz. Scale bar = 0.1mm, all figures to same scale. Abbreviations: a - aedeagus, ae - aedeagal apodeme.

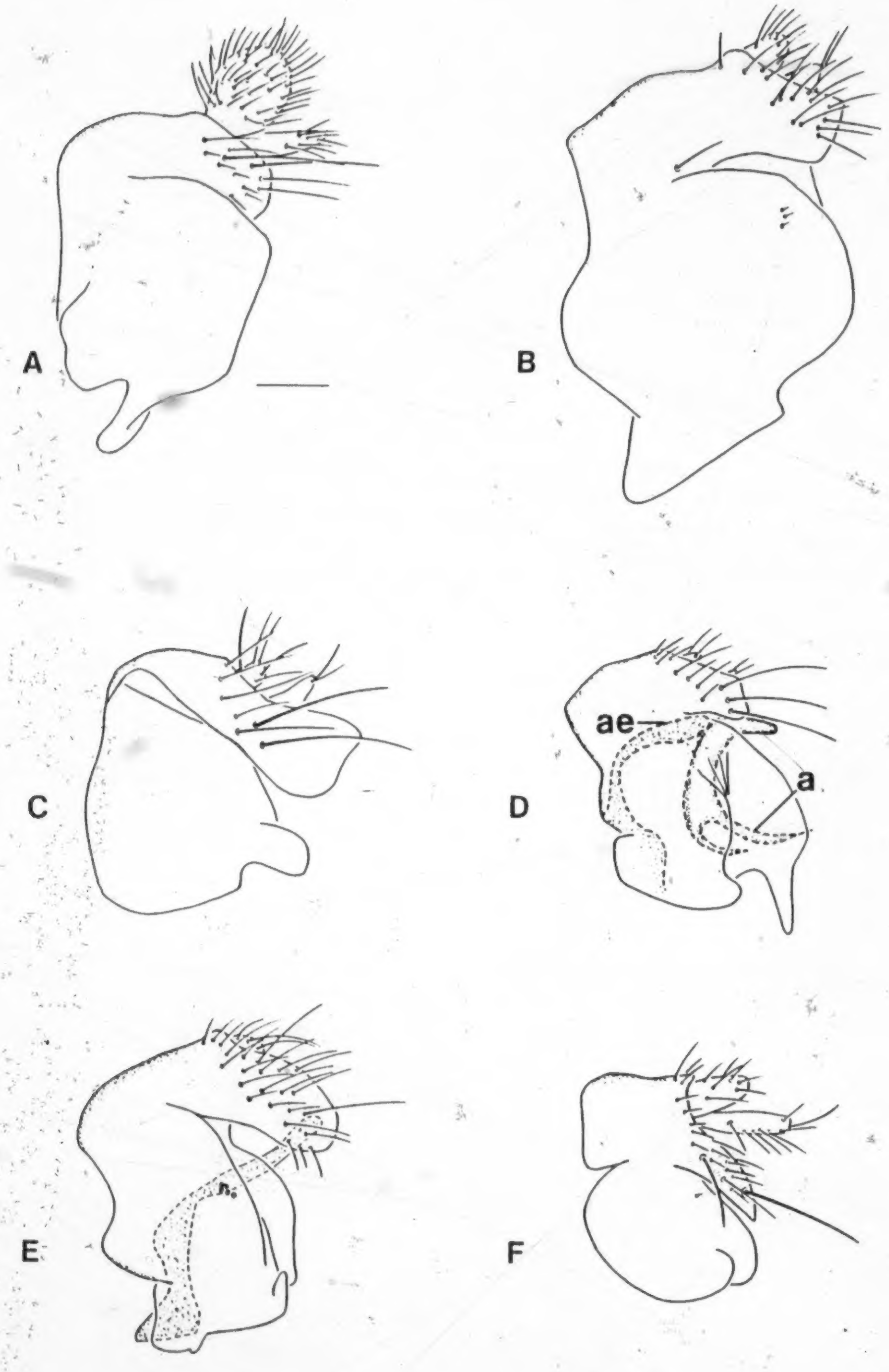

A
B
C
D
ae
a
E
F

Fig. 4.7. A-F. Wings. A, *Borophaga subsultans* (Linnaeus); B, *Godavaria minor* (Beyer); C-D. *Latiborophaga pachycostalis* (Borgmeier). C, male; D, female; E-F. *Latiborophaga* sp. E, male; F, female. Abbreviations: as - apical swelling of wing vein R_{4+5}, cs - costal swelling, d - deflection of Rs.

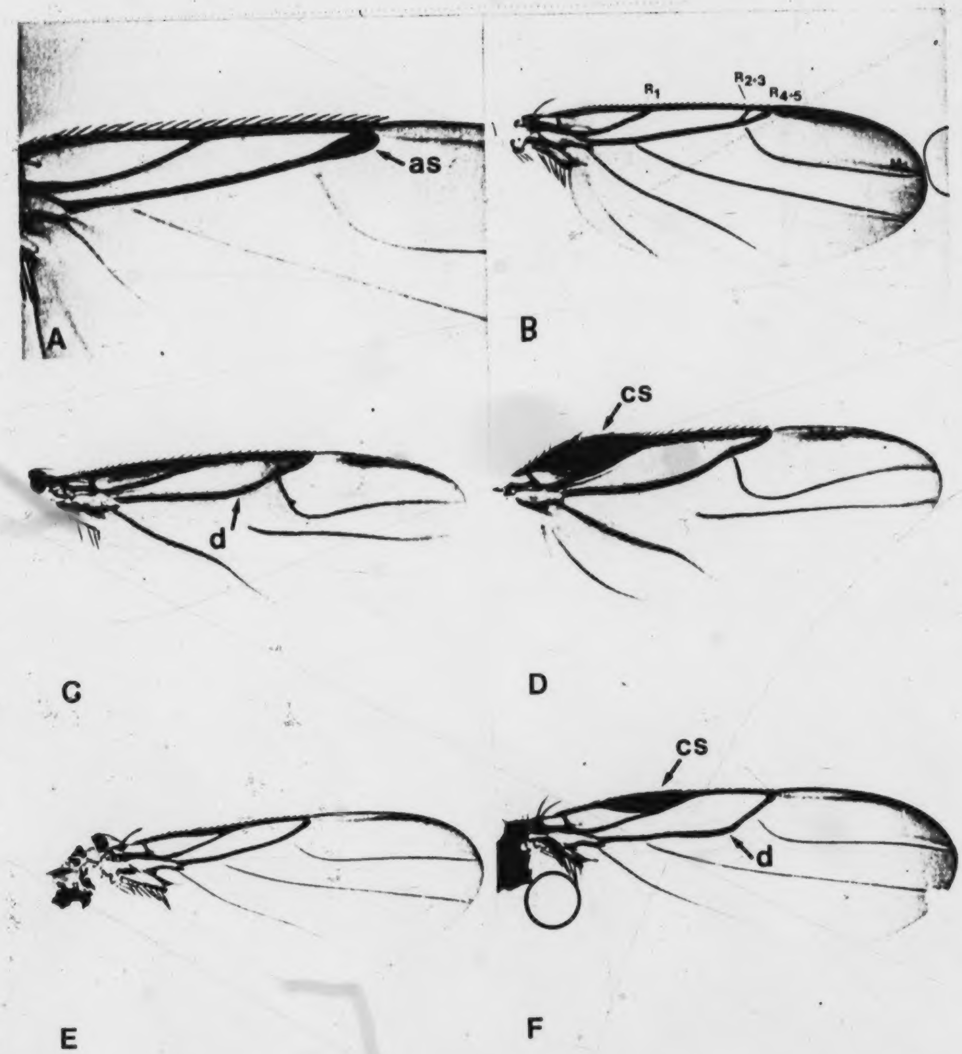

as
R1
R2+3
R4+5
A
B
cs
d
C
D
cs
d
E
F

Fig. 4.8. One equally parsimonious cladogram of the hypothesized relationships of the Hypocerinae. Character states with asterisks are homoplastic, those in parentheses are reversals.

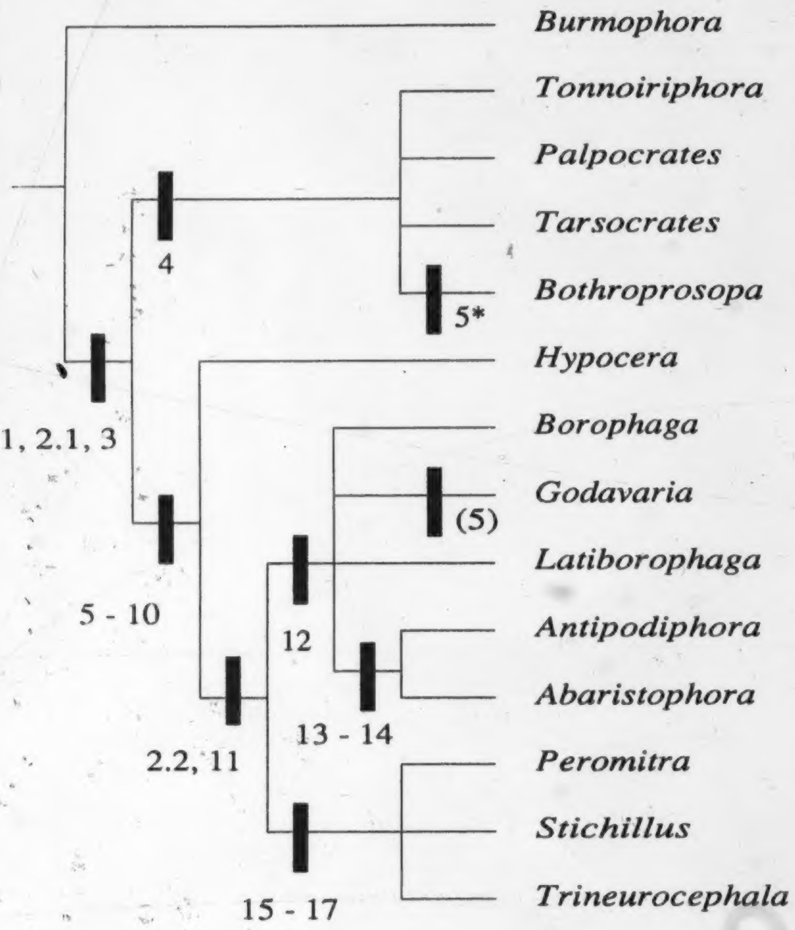
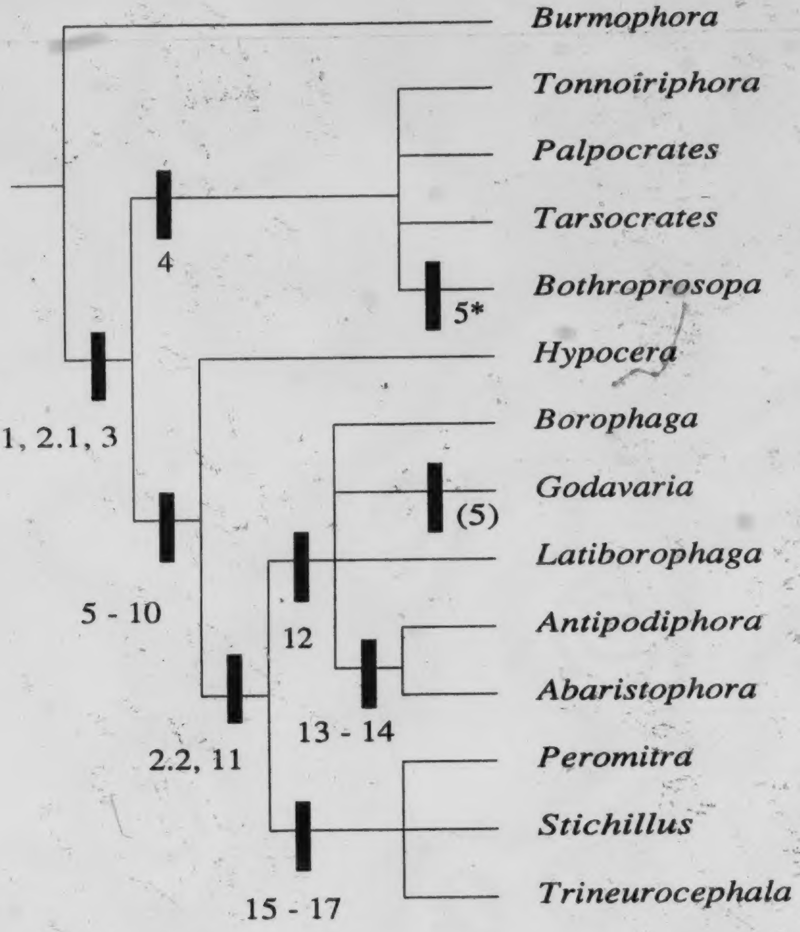

Burmophora
Tonnoiriphora
Palpocrates
Tarsocrates
Bothroprosopa
Hypocera
Borophaga
Godavaria
Latiborophaga
Antipodiphora
Abaristophora
Peromitra
Stichillus
Trineurocephala
4
5*
1, 2.1, 3
(5)
5 - 10
12
13 - 14
2.2, 11
15 - 17

Fig. 4.9. Second equally parsimonious cladogram of the hypothesized relationships of the Hypocerinae. Character states with asterisks are homoplastic, those in parentheses are reversals.


Burmophora
Tonnoiriphora
Palpocrates
Tarsocrates
Bothroprosopa
Hypocera
Borophaga
Godavaria
Latiborophaga
Antipodiphora
Abaristophora
Peromitra
Stichillus
Trineurocephala
4
5*
1, 2.1, 3
(5)
5 - 10
12
13 - 14
2.2, 11
15 - 17

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5. REVISION AND PHYLOGENETIC CLASSIFICATION OF THE NEARCTIC REGION GENERA OF THE SUBFAMILY PHORINAE (DIPTERA: PHORIDAE)

5.1 Introduction

In a review of the subfamily level classification of Phoridae (Chapter 3), I restricted the definition of the subfamily Phorinae to species of a few genera with a distinctive, presumed clasping mechanism in the male terminalia. These flies form a monophyletic group near the base of the family Phoridae, and include some of the best known taxa within the family. The relatively large-size, dark color and conspicuous leaf-running behavior of adults of the genus *Phora* Latreille bring them to the attention of many general collectors. Other genera have characteristic ways of life, for instance *Anevrina* Lioy species live in mammal burrows, whereas larvae of *Chaetopleurophora* Schmitz and *Spiniphora* Malloch eat dead snails. Because of these factors, phorines are some of the better known Phoridae; yet, the relationships among these genera, like those of most other phorids, are little known. In this paper, I present a reconstructed phylogeny and discuss the relationships of these interesting flies.

Materials and Methods

Material was examined from the following collections, the names of which are preceded by a coden, used as an abbreviation for reference to these collections (names of curators in parentheses).

BVB - collection of the author.

CNC - Canadian National Collection, Biosystematics Research Centre, Ottawa, Ontario, Canada (J.M. Cumming)

USNM - United States National Museum, Smithsonian Institution, Washington, DC, USA (F.C. Thompson)

ZFMK - Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (H.Ulrich)

Taxa from outside of the Nearctic Region frequently were used for comparison and to test hypotheses based on Nearctic specimens. Because of our limited knowledge about the Neotropical, Oriental, Australasian and Afrotropical phorid faunas, many of the species from these regions were not identified to species. This is in recognition of the incomplete coverage given by existing keys, as well as the realization that there are a great many undescribed species in regions outside of North America and Europe.

Full taxonomic synonymies are not given in this paper, except for those not found in Borgmeier (1968, 1971).

Male terminalia were examined by treatment in hot 10% KOH, and rinses of 30% acetic acid, water, and alcohol. They were then placed in an evaporating dish with a drop of glycerine and about 2ml of alcohol, and were put on a warming tray to allow the alcohol to evaporate off. Terminalia were then placed in glycerine jelly on glass slides and examined with light microscopy.

Some specimens were gold-coated and examined with a Cambridge 100 Scanning Electron Microscope.

Hypothesized relationships were reconstructed using standard cladistic techniques (Hennig, 1966). The cladogram in this paper was constructed manually, without computer algorithms. The data set subsequently was checked with the computer program Hennig-86 (Farris, 1989) to see if there were further equally parsimonious cladograms.

5.3 Terms

Recent reviews of Diptera phylogeny have postulated adelphotaxon (Griffiths, 1972), ancestor-descendant (Chvála, 1983) or no special relationship (McAlpine, 1989) between the Orthogenya and Cyclorrhapha. This disagreement affects the terms used to refer to the male genitalia, and I deal with it as I have previously (Brown, 1987).

The terms synapotypic, apotypic, plesiotypic etc. have been used in this paper as more general terms, rather than synapomorphic, apomorphic, plesiomorphic and so on that refer only to structure (Chapter 2, Terms). Other terms not used by Hennig, but subsequently proposed by Ax (1987) are used in this work: adelphotaxon (=sister-group) and groundpattern (=groundplan). The reasons for preferring the use of these more recent terms are those of Ax (1987).

5.4 Reconstructed Phylogeny of the Phorinae

Hypothesized synapotypic character states.

The phylogenetic relationships among the taxa of phorines are not well understood at this time, and warrant further study. The following are synapotypies that may be useful in classifying these genera, but more such character states are needed before a clear understanding of the relationships in this subfamily will exist. Species level revisions of the various genera are required.

Hypothesized synapotypic character states are plotted on a cladogram in Fig. 5.7 (see also Table 5.1).

1 Sternite 7 of female extended posteriorly to posterior margin of segment 8 (Figs. 5.5E-F).

2 Puparium with elongate, anteriorly directed hind spiracle.

3 Frons with median furrow.

Many other phorids have this character state present, but among primitive-grade taxa, only *Conicera* Meigen also has a median furrow. As discussed previously (Chapter 3), I treat this as a derived character state, but Disney (1988) treats it as primitive.

4 Wing vein R_{2+3} absent.

This wing vein has been lost many times in the Phoridae, but it is still most parsimonious to consider its loss here as a synapotypy.

5.5 Classification

This classification depicts the relationships of the taxa using sequencing and subordination. Taxa equally indented are adelphotaxa; when there are more than one such group they are successive adelphotaxa, unless labelled *sedis mutabilis* (Wiley, 1981).

Spiniphora-group *sedis mutabilis*
  Chaetopleurophora Schmitz
  Spiniphora Malloch

Phora-group *sedis mutabilis*

Coniceromyia Borgmeier

Phora Latreille

Anevrina Lioy *sedis mutabilis*

Plethysmochaeta Schmitz *sedis mutabilis*

5.6 Revision of genera

SUBFAMILY PHORINAE Curtis 1833

Type genus: *Phora* Latreille 1796

Notes about synonymy. This taxon formerly referred to all phorids that did not belong to the subfamilies Aenigmatiinae, Alamirinae, Metopininae, Termitoxeniinae or Thaumatoxeniinae. The present monophyletic concept of this group was proposed previously (Chapter 3).

Diagnosis. Right surstylus separate from epandrium, left surstylus fused to epandrium. Right hypandrial lobe enlarged, with two processes in species of most genera, left hypandrial lobe reduced in species of some genera.

Geographical distribution. Found in most parts of the world, except Australia.

Known fossil material. A fossil species of *Anevrina* was described from Baltic amber (Brues, 1939), and fossil *Chaetopleurophora* species are known from Baltic amber (Brues, 1939), Miocene Florissant shale (Brues, 1908, 1939), and Eocene Fushun amber (Hong, 1981). I have seen none of these specimens, however, so I cannot comment on their correct placement.

Phylogenetic relationships. In the phylogenetic classification of Brown (Chapter 3), this subfamily is the adelphotaxon of subfamilies Aenigmatiinae + Conicerinae + Metopininae.

Included Nearctic Region taxa. Anevrina Lioy, *Phora* Latreille, *Chaetopleurophora* Schmitz, *Coniceromyia* Borgmeier, *Spiniphora* Malloch.

Taxa from other zoogeographic regions. Plethysmochaeta Schmitz (Afrotropical and Oriental Region).

5.6.1 ***Chaetopleurophora* Schmitz 1922**

(Figs. 5.1B, 5.2A-E, 5.3A-E, 5.4A-E, 5.5F)

Type species: *Phora erythronota* Strobl 1892

Derivation of generic name. The name refers to the long seta on the anepisternum of some species.

Diagnosis. Anepisternum setulose, and, in most species, with long seta. Most species with enlarged setulae on hind tibia (Fig. 5.2B). Males of most species with subepandrial process.

Way of life and immature stages. Life history information is available for *C. bohemanni*, *C. erythronota*, *C. pygidialis*, and *C. spinosior* , which were reared from dead snails. Since dead snails are also the food used by larval *Spiniphora*, the adelphotaxon of *Chaetopleurophora* (below), this lifestyle can be considered a synapotypic character state.

The larva of one species, *C. pygidialis*, is described (Schmitz, 1941b), but the puparium of *C. bohemanni* (Lundbeck, 1922) and *C. pygidialis* (Schmitz, 1917, as *C. bohemanni*) are known also. The structure of the hind spiracles of the puparium of *C. pygidialis* is similar to that of *Spiniphora* species.

Phylogenetic relationships. This genus is the adelphotaxon of *Spiniphora*.

Hypothesized autapotypic character states of *Chaetopleurophora* include the following:

1 Anepisternum setulose.

2 Anepisternum with single, long seta (except some Neotropical Region species).

The male terminalia of species of this genus are extremely divergent, making phylogenetic analysis difficult. Males of all species examined apparently lack the right surstylus, although the right side of the epandrium is modified in males of some species. The presumably most primitive male terminalia are found in males of *C. atra*, *C. pennsylvanica* and *C. rubricornis*, the *C. spinosa*-group of Schmitz (1941a). This group also includes at least *C. spinosa* Schmitz, *C. spinosior* Schmitz and *C. spinosissima* Strobl, all found in Europe. Their traditional diagnostic character state is hind tibia with dorsal setae and without transverse rows of enlarged setulae, which is a primitive condition relative to other *Chaetopleurophora* males that have the transverse rows of setulae. Thus, this group probably is not monophyletic. Males of the *C. spinosa*-group species have terminalia of the following structure:

1 Left surstylus elongate, or epandrium with neomorphic process (Fig. 5.2A).

2 Long, subcercal process present that either represents an extended subepandrial plate or a dorsally-shifted right surstylus (Fig. 5.3A).

3 Right hypandrial lobe with large process, left hypandrial lobe small, as in other phorines (Fig. 5.4A).

Three other species that I examined, *C. setipes* Borgmeier, *Chaetopleurophora* sp. A and D, all from the Neotropical Region, would also fit the diagnosis of the *C. spinosa*-group. The terminalia of male specimens of these species differ from those of males of the Holarctic Region species, however, as follows:

1 Only one elongate dorsal structure present, namely a median or submedian, setose lobe that may be a modified subcercal process or a fused left surstylus + subcercal process. The evidence for this being a fusion product is a dorsal ridge that is extended along the left side of theis structure. The submedian lobe is separate from the rest of the epandrium (Fig 5.2B, 5.3B).

2 Left hypandrial process markedly enlarged, longer than right process (Fig. 5.4B).

Adults of species that have transverse rows of enlarged setulae on the dorsum of the hind tibia were called the *C. eurythronota*-group by Schmitz (1941a). Males of *C. eurythronota*, *C. rufithorax* and *C. multiseriata* are the Nearctic Region members of this group, that also includes *C. bohemanni* (Becker) and *C. pygidialis* Schmitz from Europe. The male terminalia of *C. bohemanni*, *C. erythronota*, *C. pygidialis* (figured in Schmitz, 1941a) and *C. multiseriata* show markedly different structure. The male terminalia of *C. pygidialis* (Schmitz, 1941a, Figs. 88a, b) are as follows:

1 Left surstylus elongate (as in Fig. 5.2A).

2 Long subcercal process present (as in Fig. 5.3A).

3 Left hypandrial lobe small, right hypandrial lobe with long process (as in Fig. 5.4A).

The male terminalia of the type species of the genus, *C. erythronota* (Figs. 5.2C, 5.3C, 5.4C), are similar, except that there is no elongate subcercal process present (Fig. 5.3C) and the hypandrial lobes are subequal (Fig. 5.4C) in ventral view.

The male terminalia of *C. multiseriata* and a similar, undescribed species from Chile are dissimilar to those of all other examined species, as follows:

1 Left surstylus short (Fig. 5.2D).

2 Long subcercal process absent (Fig. 5.3D).

3 Hypandrial lobes subequal (Fig. 5.4D).

4 Aedeagus of special structure, unlike that of any other examined species.

Finally, the hind tibia of the Neotropical Region species *C. semifurcata* Borgmeier is unusual, as both dorsal setae and transverse rows of enlarged dorsal setulae are present. The male terminalia of this species closely resemble the terminalia of males of the genus *Coniceromyia*, as follows:

1 One large dorsal process present, apparently in the form of left surstylus, but

probably derived from the laterally shifted subcercal process (Figs. 5.2E, 5.3E).

2 Hypandrial lobes subequal (Fig. 5.4E).

Examination of the female terminalia of Holarctic Region species shows a further interesting character state, the presence of a single, median sternite 7 that is extended to the posterior margin of segment 8. This state is present also in females of the genus *Spiniphora*, and is an important synapotypy linking these two genera. Females of all species of Neotropical Region *Chaetopleurophora* that I examined lack this sclerite, as do female *C. multiseriata*. If this character state is accepted as a valid synapotypy of Holarctic Region *Chaetopleurophora* + *Spiniphora*, and the Neotropical Region species are excluded, then the genus *Chaetopleurophora* is rendered paraphyletic. Unfortunately, a species level revision is needed to determine whether the Neotropical Region species of this genus are relatively primitive, or relatively derived. I believe that they are in fact relatively derived, and that the following scenario has occurred:

1 Primitive character states for *Chaetopleurophora* include female sternite 7 extended to posterior margin of segment 8; male with left surstylus fused to epandrium, elongate subcercal process present that is in fact the medially shifted right surstylus; right side of hypandrium with elongate process (as in Figs. 5.2A, 5.3A, 5.4A).

2 *C. multiseriata* and the similar, undescribed species from Chile represent a

derived offshoot of this pattern, that have female terminalia without sternite 7, but with unusual tergite 7 with long, internal, anteriorly directed rod; left surstylus reduced; subcercal process reduced; hypandrial lobes subequal, without processes.

3 Neotropical Region species are derived as follows: female without sternite 7; left surstylus lost or fused to subcercal process; subcercal process (right surstylus) enlarged, shifted to left side of epandrium in *C. semifurcata* and appearing to be an articulated left surstylus; hypandrial lobes modified, with up to three long processes; males of some species with terminalia rotated 90° clockwise.

In this, and any other scenario that advocates a monophyletic genus *Chaetopleurophora*, the transverse rows of enlarged setulae found on the mid- and hind tibiae have either evolved more than once, or have been lost in some species. Hopefully, a phylogenetic revison of this genus will shed light on these character states.

Number of recognized species. Twenty-two.

Nearctic Region material examined. ***C. atra*** **Borgmeier**, CANADA: Ontario: Guelph, South Arboretum, 1♂, 15-23.v.1984, 1♂, 27.iv.-2.v., 1♂, 11-16.v.1985, B.V.Brown, intercept trap in forest, Malaise trap at forest edge (BVB), Stouffville, 3♂, 5-13.v.1983, 2♂, 21-28.iv., 5♂, 28.iv.-5.v., 2♂, 1♀, 5-12.v., 1♂, 12-26.v.1985, B.V.Brown, Malaise head, Malaise pans (BVB), UNITED STATES: Washington: 1♂, 1♀ [*in copula*], Jefferson Co., Clearwater, 25.vi.1987, B.V.Brown, rainforest (BVB), 4♂, Whatcom Co., 8km S Bellingham, 1.vi.-3.vii.1986, B.Brown & T.Spanton, FIT, cedar/ aspen (BVB); ***C. eurythronota* (Strobl)**, CANADA: Ontario: Guelph, 23♂, 5♀, South Arboretum, various dates from 19.vi.-26.ix, B.V.Brown, intercept trap, water traps, Malaise traps (BVB), 1♀, Leamington, Point Pelee National Park, 17.vii.1985, B.V.Brown (BVB); ***C. multiseriata* (Aldrich)**, CANADA: Ontario: 1♂, 1♀, Guelph, South Arboretum, 13-22.vii.1985, B.V.Brown, Malaise trap (BVB), 2♂, 1♀, Leamington, Point Pelee National Park, 14.vi.1984, B.V.Brown (BVB), UNITED STATES: Arizona: Cochise Co., near Portal, S.W.R.S., 1♀, 22.vii., 1♂, 27.vii., 1♂, 2♀, 29.vii., 1♀, 31.vii., 1♂, 8.viii., 2♂, 12.viii., 1♀, 14.viii., 1♂, 18.viii., 1♂, 29.viii.1965, V.Roth, Malaise, 1♀, 18-23.viii.1984, B.V.Brown, water traps (BVB); ***C. pennsylvanica* (Malloch)**, CANADA: Ontario: 1♂, Guelph, South Arboretum, 11-15.iv.1985, B.V.Brown, Malaise trap at forest edge (BVB), Stouffville, 3♂, 21-28.iv., 1♂, 28.iv.-5.v.1985, B.V.Brown, Malaise head (BVB); ***C. rubricornis* Borgmeier**, CANADA: Ontario, Guelph, South Arboretum, 1♂, 1♀, 23.v.-2.vi.1984, 1♀, 16-22.v., 1♂, 22-24.v.1985, B.V.Brown, intercept trap, Malaise trap (BVB), 1♀, Stouffville, 5-13.v.1983 (BVB).

Material examined from other zoogeographic regions. ***C. bohemanni* (Becker)**, 1♂, GERMANY: Gross Raum, 15.v.1932, P. Speiser (ZFMK), 1♀, Berlin, Grunewald, 2.vi.1951 (ZFMK); ***C. pygidialis*** **Schmitz**, 1♂, NETHERLANDS: Maastricht, 13.iii.1908, H.Schmitz, from *Helix* (ZFMK), 1♀, Valkenburg, H.Schmitz (ZFMK); ***C. spinosior*** Schmitz, 1♂, IRELAND: Tullabeg, v.1939 (ZFMK), 1♀, Körösmezö, Kertész (ZFMK); ***C. spinosissima*** **(Strobl)**, 1♂, POLAND: Nimptsch, Schls., Duda (ZFMK), 1♀, NETHERLANDS: Valkenburg, H.Schmitz (ZFMK); ***C. semifurcata*** **Borgmeier**, COSTA RICA: Heredia, Puerto Viejo de la Sarapiquí, La Selva Biological Station, 40m, 1♂, 16-23.v., 3♂, 23-26.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50 (BVB), 1♂, Puntarenas, Monteverde, Finca Canada, 28.v.-1.vi.1988, 1700m, Malaise trap, B.V.Brown, clearcut edge (BVB), ECUADOR: 1♀, Napo, Tena, 20-27.v.1987, 500m, B.V.Brown, windows (BVB), Pichincha, 47km S Santo Domingo, Rio Palenque Science Center, 2♂, ii.1983, Masner & Sharkey, Malaise trap, 1♂, 1♀, 29.iv.-5.v.1987, B.Brown & L.Coote, Malaise trap, rain forest, 180m (BVB), JAMAICA: 1♂, Olar, Portland Ridge, 11-15.viii.1974, S.Peck, forest (BVB), MEXICO: 2♂, Jalisco, Chamela, 13.xi.1985, Malaise trap (BVB), TRINIDAD: 1♂, Arima Valley, Simla Station, 2-10.vi.1977, Malaise trap, P.Feinsinger (BVB), VENEZUELA: 1♂, Zulia, 200m, 20-23iv.1981, Townes & Masner, Malaise trap, rain forest (BVB); ***C. setipes*** **Borgmeier**, COSTA RICA: 2♂, Heredia, Puerto Viejo de la Sarapiquí, La Selva Biological Station, 40m, 16-23.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50 (BVB); ***Chaetopleurophora*** **sp. A**, 2♂, Pichincha, 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown & L.Coote, Malaise trap, rain forest, 180m (BVB), 1♂, 17km E Santo Domingo, Tinalandia, 6-13.v.1987, B.V.Brown, 710m, clubhouse windows (BVB); ***Chaetopleurophora* sp. B**, COSTA RICA: 1♂, 1♀, Puntarenas, road to Rincon, 24km W Pan American Highway, 200m, iii-iv.1989, Malaise trap, P.Hanson & I.Gault (BVB); ***Chaetopleurophora* sp. C**, COSTA RICA: 1♀, La Selva, Puerto Viejo, ii.1980, W.Mason (BVB); ***Chaetopleurophora* sp. D**, COSTA RICA: 1♂, Pandora, Estrella Valley, 28.iii.1984, G.V.Manley, Malaise trap (BVB); ***Chaetopleurophora* sp. E**, 1♂, CHILE: Osorno, Puyehue National Park, *ca.* Anticura, 13.ii.1988, L.Masner, *Nothophagus* forest, sweep sample (BVB).

5.6.2 *Spiniphora* **Malloch 1909**

(Figs. 5.5A-B, 5.5E, 5.6A)

Type species: *Phora maculata* Meigen 1830_(designated by Malloch 1910)

Derivation of generic name. From the Latin for spine or thorn, presumably referring to the long setae on the legs.

Diagnosis. Frons without median furrow; wing vein R_{2+3} present; hind tibia without enlarged setulae; female with lateral sclerites on segment 7; sternite 7 extended to posterior margin of segment 8; male terminalia with right surstylus separate, downturned.

Way of life and immature stages. Five species have been reared from dead snails (e.g. Achterberg & Bin, 1981; Disney, 1972, 1976; Grensted, 1956; Lundbeck, 1920; Schmitz, 1917), but *S. bergenstammi* breeds in other situations, such as birds' nests, improperly washed milk bottles (Disney 1983). Three adult males and one adult female of *S. excisa* were collected in mushroom-baited pitfall traps (Brown & Marshall, 1984), but as these were the only specimens collected in two summers of trapping, it seems that this was a chance association.

Immature stages of several species have been described (Schmitz, 1941a).

Collecting methods. I have collected specimens of this genus only in Malaise traps (except for *S. excisa*, above).

Geographical distribution. Holarctic Region, Oriental Region; one species (*S. bergenstammi*) in the Neotropical Region (Borgmeier, 1968) and New Zealand (H. Oliver, personal communication) was probably introduced by humans.

Chorological affinities. Two species found in the Nearctic Region, *S. bergenstammi* and *S. excisa*, are also found in Europe. At least *S. bergenstammi* was probably introduced into North America, as it is a general scavenging species according to Dr. J.K. Barnes (Biological Survey, Albany, New York, USA, personal communication), who is rearing this species to determine life history parameters. Larvae of *S. excisa* eat dead snails (Lundbeck, 1920).

Phylogenetic relationships. This genus is the adelphotaxon of *Chaetopleurophora* (see above).

The right surstylus and right hypandrial lobe of males of *S. trispinosa* are unusual in appearence compared to those of other species. Males of *S. bergenstammi*, *S. excisa*, *S. maculata*, *S. signata*, *S. slossonae*, and *S. spinulosa* have the right surstylus elongate and ventrally directed (Fig. 5.6A), and the right hypandrial lobe has a socket-like concavity to receive the surstylus (Figs. 5.5A-B). The right surstylus of males of *S. trispinosa*, in contrast, is short, and the hypandrial process is relatively unmodified. Whether this is a character state reversal, or the male terminalia of *S. trispinosa* are primitive, remains to be determined.

Based on larval structure, Schmitz (1935) divided the genus into two groups: the *S. bergenstammi*-group and the *S. maculata*-group. The *S. bergenstammi*-group have large papillae with long setae dorsally and dorsolaterally on larval abdominal segments 1-7, while the *S. maculata* group have bare abdominal segments or at most small marginal papillae with short setae. These two groups are probably not monophyletic with respect to each other, with the *S. bergenstammi*-group the derived clade and the *S. maculata*-group the primitive, paraphyletic residue. Among Nearctic species, *S. bergenstammi* and *excisa* belong to the *S. bergenstammi*-group (according to Schmitz, 1935), while the larvae of the other three species are unknown. The larval structure doubtlessly will be important in determining the relationships between groups, and it will be interesting to see if the possibly primitive terminalia of males of *S. trispinosa* correspond with a primitive (*S. maculata*-group) larva.

Hypothesized autapotypic character states of *Spiniphora* include the following:

1 Female with tergite 7 present, extended laterally.

Number of recognized species: Total of twenty; five are found in the Nearctic Region.

Nearctic Region material examined. ***S. excisa*** **(Becker)**, 8♂, 1♀, CANADA: Ontario: Guelph, South Arboretum, 17-24.vi.1983, 24-28.vi.1983, 22-24.v.1985, 24-30.v.1985, 24-28.vi.1984, 10-14.viii.1985, 9-13.vii.1985, 13-22.vii.1985, B.V.Brown, Malaise trap, mushroom-baited pitfall traps, deciduous forest (BVB); ***S. slossonae*** **(Malloch)**, 7♂, CANADA: Ontario: Guelph, South Arboretum, 20.vi-21.vii.1984, 25.vi-3.vii.1985, 27.viii-4.ix.1985, 4-11.ix.1985, Malaise trap, flight-intercept trap, deciduous forest (BVB); *S. spinulosa* **(Malloch)**, 1♂, CANADA: Ontario: Guelph, South Arboretum, 27.iv-2.v.1985, B.V.Brown, Malaise trap at forest edge (BVB); ***S. trispinosa*** **(Malloch)**, 2♂, CANADA: British Columbia: North shore Shuswap Lake, 50° 59'N, 119°, 06'W, 23-31.viii.1987, 400m, J.E.O'Hara, Malaise trap, columbian forest (BVB), USA: 1♂, Oregon: Josephine Co., 10mi. N Grants Pass, 3.vi-1.vii.1986, B.Brown & T.Spanton, pine/ oak, FIT (BVB), 1♂, Washington: Jefferson Co., Olympic National Park, Queets River Road, 22-24.vi.1987, B.V.Brown, Malaise trap, rain forest (BVB).

Material examined from other zoogeographic regions. *S.* ***bergenstammi*** **(Mik)**, 3♂, WEST GERMANY: Ingelheim am Rhein, 1-21.vii.1965, Malaise trap (CNC); *S.* ***dorsalis*** **(Becker)**, 1♂, ENGLAND: Devon, Torquay, 15.vi.1960, J.R.Vockeroth (CNC); *S.* ***maculata*** **(Meigen)**, 1♀, ENGLAND: Oxford, ii.1953, J.R.Vockeroth (CNC), 1♂ NETHERLANDS: Sittard, 4.iv.1916, from *Helix* (ZFMK); ***S. signata*** **(Schmitz)**, 1♂, 1935, P. Remo (ZFMK).

5.6.3 *Coniceromyia* Borgmeier 1923

(Fig. 5.5C, 5.6B)

Type species: *Coniceromyia epicantha* Borgmeier 1923 (original designation).

Derivation of generic name. Named for the elongate, pointed first flagellomere.

Diagnosis. Flagellum 1 elongate in males. Male with fore basitarsus modified. Fore tarsomeres broad. Costa thick. Hind femur with ventrobasal spinuli.

Way of life and immature stages. Unknown. A series of an undetermined species of this genus in the University of California, Berkeley, Collection of Insects was labelled "reared from dead snails", but this record needs further verification.

Collecting methods. These flies are collected in small numbers by Malaise traps.

Geographical distribution. Most species are found in the Neotropical Region, but two are found in the Nearctic Region.

Phylogenetic relationships. This genus is the adelphotaxon of *Phora.* The two genera are linked by two character states that are subject to much homoplasy within the family; thus, the evidence for their adelphotaxon relationship is tenuous.

Hypothesized autapotypic character states of *Coniceromyia* include the following:

1 Male forebasitarsus modified, with thin process.

2 Flagellomere 1 elongate (in most, but not all species).

3 Costa thickened.

Number of recognized species: Total of thirty-one; two are found in the Nearctic Region.

Nearctic Region material examined. ***C. arizonensis*** **Borgmeier**, USA: **Arizona**: Cochise Co., 11♂, near Portal, S.W.R.S., 18.vii.-8.viii.1965, V.Roth, Malaise trap (BVB), 1♂, 1♀, 18.5km W. Portal, Basin Trail head, 8-10.vii.1987, yellow pans, B.Brown & T.Spanton, 1950m, oak/ pine/ juniper (BVB), 1♂, 12.5km S. Sierra Vista, Ramsey Canyon, 28.vii.-2.viii.1986, B.V.Brown, Malaise trap, 1700m, oak/ pine/

juniper (BVB), 14km S. Sierra Vista, Carr Canyon Road, 10-11.vi.1987, B.V.Brown, oak forest, yellow pans (BVB).

Material examined from other zoogeographic regions. ***C. atricolor*** **Schmitz**, 1♂, CHILE: Llanquihue, Casa Pangue, 4-10.xii.1926, F.& M.Edwards (ZFMK); ***C. fusca*** **Borgmeier**, 1♂, VENEZUELA: **Merida**: S. of Bolivar National Park, La Aguada, 13.v.1981, L.Masner, 3000m, Malaise trap (BVB); ***C. latimana*** **(Malloch)**, 1♂, WEST INDIES: **Nevis**: Dascent's Estate, 28.viii.-21.ix.1985, L.Coote and T.Blanchette, Malaise trap, citrus orchard (BVB), **St. Kitts**: Wingfield Mt., 400m, 4♂, 1-31.x., 2♂, 1-30.xi.1985, L.D.Coote, Malaise trap, old field/ forest (BVB); ***C. plaumanni*** **Borgmeier**, 1♂, ECUADOR: **Napo**: Tena, 20-27.v.1987, 500m, B.V.Brown, windows (BVB).

5.6.4 *Phora* Latreille 1796

(Fig. 5.1A)

Type species: *Musca aterrima* Fabricius 1794 [junior homonym, preoccupied by *aterrima* Villers 1789, = Trineura atra Meigen 1804] (subsequent monotypy, Latreille, 1802).

Derivation of generic name: According to Schmitz (1938), *phora* is a Greek word for quick movement, describing the rapid, jerky, darting run of the adult fly. Brown (1956) lists *phor* as Greek for thief, but Schmitz' definition is probably closer to what was intended by Latreille.

Diagnosis. Dark, velvety black phorids (although sometimes brown, or tinged with green); eye enlarged, gray; left hypandrial lobe reduced. Once seen, these distinctive flies are easily recognized.

Way of life and immature stages. The immatures and larval food of only one species, *P. holosericea* Schmitz, have been discovered and crudely figured (Yarkulov, 1972); immatures of this species are predators of root aphids on a variety of plants. Adults are well known to run on the leaves of undergrowth plants in the typical, jerky, phorid manner, and are one of the most commonly observed Nearctic Region phorids, especially in the north. Males form aerial swarms under the boughs of trees, especially conifers (Gotô, 1984; personal observation).

Collecting methods. The adults are easily collected by aspirating individuals from leaves, netting aerial swarms, and especially by collecting with Malaise traps.

Geographical distribution. Found mostly in the Holarctic Region, but some species reach into the Neotropical and Oriental Regions at higher elevations.

Phylogenetic relationships. This genus is the adelphotaxon of *Coniceromyia.*

Hypothesized synapotypic character states of *Phora* include the following:

1 Males with eye enlarged, frons narrow (Fig. 5.1A).

2 Body velvety black, possibly resulting from structure of minute cuticular structures (Gotô, 1984, Fig. 1c).

The cuticular "blackening" setulae of *Phora* adults are also found in adults of *Conicera* Meigen (Conicerinae) species, and some species of *Triphleba* Rondani (Metopininae).

Number of recognized species. Fifty-three; fourteen are found in the Nearctic Region.

Material examined. As Gotô (1984, 1985a, b, c, 1986) has revised thoroughly the Japanese species, and provided many excellent illustrations of important characters, it was unnecessary to examine many Nearctic specimens. I examined several, undetermined species.

5.6.5 *Anevrina* Lioy 1864

(Figs. 5.5D, 5.6C)

Type species: *Phora urbana* Meigen 1830 (Coquillett, 1910; by inference as the "first species" listed by Lioy).

Derivation of generic name. According to Lioy (1864) this name refers to the weak anal vein of the wing.

Diagnosis. Wing vein R_s setulose.

Way of life and immature stages. Some species of this genus collected at Malaise traps in Guelph, Ontario were present only in the spring (*A. olympiae* and *A. spinipes*), and are thus probably univoltine. Other species (*A. thoracica* and *A. variabilis*, for example) do not follow this pattern. Adults of *A. thoracica*, *A. unispinosa* (Zetterstedt) and *A. urbana* have been reported from mammal nests (Baumann, 1977; Hackman, 1963a, b; Lundbeck, 1922; Malloch, 1908) and are attracted to carrion (Lundbeck, 1922), as are those of *A. luggeri* and *A. macateei* (personal observation). Adults of *A. variabilis* has been collected in burrows of northern pocket gophers, *Thomomys talpoides* (Richardson), (unpublished data) in Alberta, Canada, and was reported as associated with the same species in California (Borgmeier, 1963). Adults of *A. sulcatifemur* were reported from a "gopher burrow" in California (Borgmeier, 1963) and those of *A. spinipes* were collected in burrows of *Marmota monax* (Linnaeus) in Ontario (below, material examined).

These records of adults in mammal burrows, combined with the attraction of carrion to certain species, indicate that larvae of species of *Anevrina* feed on dead animals or debris in mammal burrows. Univoltine species probably breed in rodents that die during winter.

Descriptions of larvae and puparia are given by Schmitz (1941a).

Collecting methods. Males are collected with Malaise traps, but females may be more easily captured with carrion traps set near mammal burrows. Digging out mammal burrows, or setting carrion traps inside of burrows, also can be successful.

Geographical distribution. Specimens of *Anevrina* species have been collected in the Holarctic and Oriental Regions.

Phylogenetic relationships. Unknown.

Hypothesized autapotypic character states of *Anevrina* include the following:

1 Wing vein R_s setulose.

2 Process of subepandrial plate convoluted.

Number of recognized world species. Total of fourteen; nine are found in the Nearctic Region.

Nearctic Region material examined. ***A.luggeri*** **(Aldrich), 6♂**, CANADA: **Ontario**: Guelph, South Arboretum, 30.v.-5.vi., 11-19.vi., 19-24.vi., 25.vi.-3.vii., 9-13.vii.1985, B.V.Brown, Malaise trap at forest edge, Malaise trap in wet shrubby meadow (BVB), 1♀, 11-13.vii.1984, B.V.Brown, carrion trap (BVB), 2♂, Stouffville, 3-10.vi., 14-20.viii.1983, B.V.Brown, Malaise pans (BVB); ***A. macateei* (Malloch)**, 2♂, CANADA: **Alberta**: Edmonton, University of Alberta Ecological Reserve, 12-20.vi.1986, 5-14.vii.1986, B.V.Brown, Malaise trap, spruce/poplar/alder (BVB), **Ontario**: Guelph, South Arboretum, 19♂ collected from 2.v. until 27.viii.1985, B.V.Brown, Malaise trap at forest edge, Malaise trap in deciduous forest, Malaise trap in wet shrubby meadow (BVB), 1♂, 11-13.vii.1984, B.V.Brown, carrion trap (BVB), 3♂, Heron Bay, Pukaskwa National Park, 25-27.vii.1985, B.V.Brown, Malaise trap, spruce/juniper forest (BVB), 1♂, Stouffville, 12-26.v.1985, B.V.Brown, Malaise trap (BVB), 2♂, USA: **Arizona**: 1♂, Cochise Co., near Portal, S.W.R.S., 29.vii.1965, V.Roth, Malaise trap (BVB), 1♂, Coconino Co., 7000', Coconino National Forest, 11 mi. N. Flagstaff, Bonito Park, Mt. meadow, 6-7.viii.1984, carrion, L.B.Carlson (BVB), **Washington**: Jefferson Co., Olympic National Park, Queets River Road, 22-24.vi.1987, B.V.Brown, Malaise trap, rain forest (BVB), 2♂, Whatcom Co., 8km S. Bellingham, 1.vi-3.vii.1986, B.Brown & T. Spanton, FIT, cedar/ aspen forest (BVB); ***A. olympiae* (Aldrich)**, CANADA: **Ontario**: Guelph, South Arboretum, 1♂, 7-11.v., 2♂, 11-16.v., 1♂, 24-30.v., 2♂, 30.v.-5.vi., 1♂, 7-11.vi., 1♂, 11-19.vi., 2♂, 19-24.vi.1985, B.V.Brown, Malaise trap at forest edge, Malaise trap in deciduous forest, Malaise trap in wet, shrubby meadow (BVB); ***A. spinipes* (Coquillett)**, CANADA: **Ontario**: Guelph, South Arboretum, 1♂, 11.iv.1984, B.V.Brown, pan trap (BVB), 1♂, 4♀, 11.iv.1984, B.V.Brown, groundhog [*Marmota monax* (Linnaeus)] burrow (BVB), 2♂, 22-27.iv., 10♂, 30.iv.-2.v., 4♂, 2-11.v., 4♂, 11-15.v.1985, B.V.Brown, Malaise trap at forest edge, Malaise trap in wet, shrubby meadow (BVB), Stouffville, 2♂, 21-28.iv.1985, 1♂, 5-12.v.1985, B.V.Brown, Malaise trap (BVB); *A.* ***sulcatifemur*** **Borgmeier**, USA: **California**: Tuolumne Co, 1♂, 6km NE Tuolumne, River Ranch Campground, 22-26.vi.1986, B.V.Brown, Malaise trap, oak forest/ field (BVB), 3♂, 1.5km E. Tuolumne, 15-26.vi.1986, 750m, B.V.Brown, Malaise trap, oak foothill forest (BVB); ***A. thoracica*** **(Meigen)**, CANADA: **Alberta**: Edmonton, University of Alberta Ecological Reserve, 1♂, 26-29.v., 2♂, 29.v.-5.vi., 1♀, 5-12.vi.1986, B.V.Brown, Malaise trap, spruce/ poplar/ alder forest (BVB), **Ontario**: Guelph, South Arboretum, 1♂, 16-22.v., 1♂, 22-28.vi.1985, B.V.Brown; Malaise trap at forest edge (BVB), 1♂, USA: **Washington**: Jefferson Co., Olympic National Park, Queets River Road, 22-24.vi.1987, B.V.Brown, Malaise trap, rain forest (BVB), 1♂, Skagit Co., 24km SE Marblemount, Mineral Park, 18-20.vi.1987, B.V.Brown, Malaise trap, 500m, douglas fir/ cedar/ maple (BVB); ***A. variabilis*** **(Brues)**, USA: **California**: 2♂, Alpine Co., 1 mi. S. Monitor Pass, 8200', 22-23.viii.1979, Malaise trap, 9A-5P, M Wasbauer, P. Adams (BVB), 2♀, Tuolumne Co., 1.5km E. Tuolumne, 15-26.vi.1986, 750m, B.V.Brown, T.G.Spanton, Malaise trap, FIT, oak foothill forest (BVB).

5.6.6 *Plethysmochaeta* Schmitz 1924

Type species: *Hypocera vectabilis* Brues 1913 (by original designation).

Derivation of generic name. The name probably refers to the group (*plethys*) of setae on tergite 6 (see Schmitz, 1953, Fig. 4).

Diagnosis. Anepisternum setulose. Wing vein R_{2+3} absent. Abdominal tergite 5 of male extremely short; other abdominal structures distinctive (Schmitz, 1953, Fig. 4, Schmitz, 1958, Fig. 1); tergite 6 with medial group of long setae.

Way of life and immature stages. Brues (1913) recorded the type species as having been reared from dried Coleoptera specimens. Other species are saprophagous (Schmitz, 1953).

Collecting methods. Unknown.

Geographical distribution. Afrotropical and Oriental Regions.

Phylogenetic relationships. Unknown.

Number of recognized species. Ten.

Material examined. ***Plethysmochaeta* spp.** 1♂, MADAGASCAR: Fianarantsoa, 7km W Ranomafana, 1100m, 1-7.xi.1988, W.E. Steiner (BVB); 1♂, NIGERIA: Ibadan, 6.vii.1962, D.C.Eidt, Malaise trap (CNC).

5.7 Structural and possible functional evolution of male terminalia.

An analysis of the evolution of the male terminalia of the taxa included in the Phorinae is not yet possible. The adelphotaxon relationships among the species of the genus *Chaetopleurophora*, especially, must be established in order to gain insight into the evolution of various structures. The structural and functional aspects of these structures, as I understand them now, however, are presented below on a genus by genus basis.

Chaetopleurophora - The species of this genus are discussed above. The subcercal process of many species is probably homologous with the right surstylus of *Spiniphora* and other species.

Spiniphora - In males of *Spiniphora* species, the right surstylus is elongate and ventrally directed, inserting in a right hypandrial lobe that is bilobed, and, in some species, extensively modified. The left surstylus is fused to the epandrium, and is relatively short and unmodified. Males of *S. trispinosa* and *S. dorsalis* have relatively short right surstyli and correspondingly less modified right hypandrial processes.

Coniceromyia - Males of *Coniceromyia* species have an elongate process on the left side of the epandrium, that seems incapable of touching the bilobed right hypandrial process, but nevertheless opposes it. I hesitate to refer to the epandrial process as a left surstylus, because the form of this structure is almost identical to the epandrial process of *Chaetopleurophora semifurcata*, having a broken connection with the epandrium dorsally. This epandrial process in *Chaetopleurophora semifurcata* is probably in turn derived from the subcercal process found in male terminalia of other *Chaetopleurophora* species.

Phora - Males of *Phora* species have the left and right surstylus elaborated as a pair of forceps, similar to those of *Anevrina*, described below. In species of *Phora*, however, the ventral lobes of the forceps are smaller and not ventrally directed. The right hypandrial process again seems to receive the right forceps.

Anevrina - In males of *Anevrina*, the left surstylus, right surstylus and subepandrial plate have become elaborated as a pair of "forceps" that include a dorsal pair of posteriorly directed lobes and a ventral pair of ventrally directed lobes. The bilobed right hypandrial process seems to receive the right ventral lobe of the dorsal forceps.

Plethysomochaeta - The male terminalia of species of *Plethysmochaeta* are extremely similar to those of *Coniceromyia* species.

5.8 Suggestions for future work

The array of character states discussed above is extremely confusing, and warrants further study. In particular, we need to know if the transformation series of a right surstylus moving medially, and then left laterally in *Chaetopleurophora semifurcata* has indeed occurred, and if the epandrial structure of *Coniceromyia* species represents a continuation of this trend. The answers to these questions would have profound effects on the classification and generic concepts in this least resolved phorid subfamily.

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Table 5.1. Distribution of plesiotypic and synapotypic character states among genera of the Phorinae. 0 - plesiotypic, 1 - synapotypic.

Characters	1234
Taxa	
Chaetopleurophora	1100
Spiniphora	1100
Coniceromyia	0011
Phora	0011
Anevrina	0000
Plethysmochaeta	0000

Fig. 5.1. A, *Chaetopleurophora erythronota* (Strobl), hind tibia, dorsal; B, *Phora* sp., male, frons. Abbreviations: f - frontal furrow.

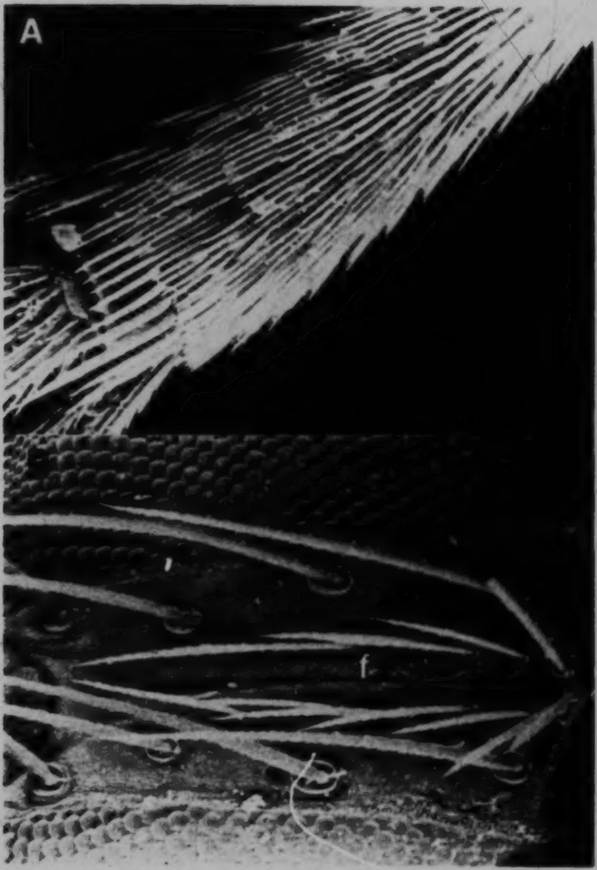

A
f

Fig. 5.2. Male terminalia, left lateral. A, *Chaetopleurophora pennsylvanica* (Malloch); B, *Chaetopleurophora* species D (Costa Rica); C, *C. erythronota* (Strobl); D, *C. multiseriata* (Aldrich); E, *C. semifurcata* (Borgmeier). Scale bar = 0.1mm, all figures to same scale. Abbreviations: l - left surstylus, s - subepandrial process.

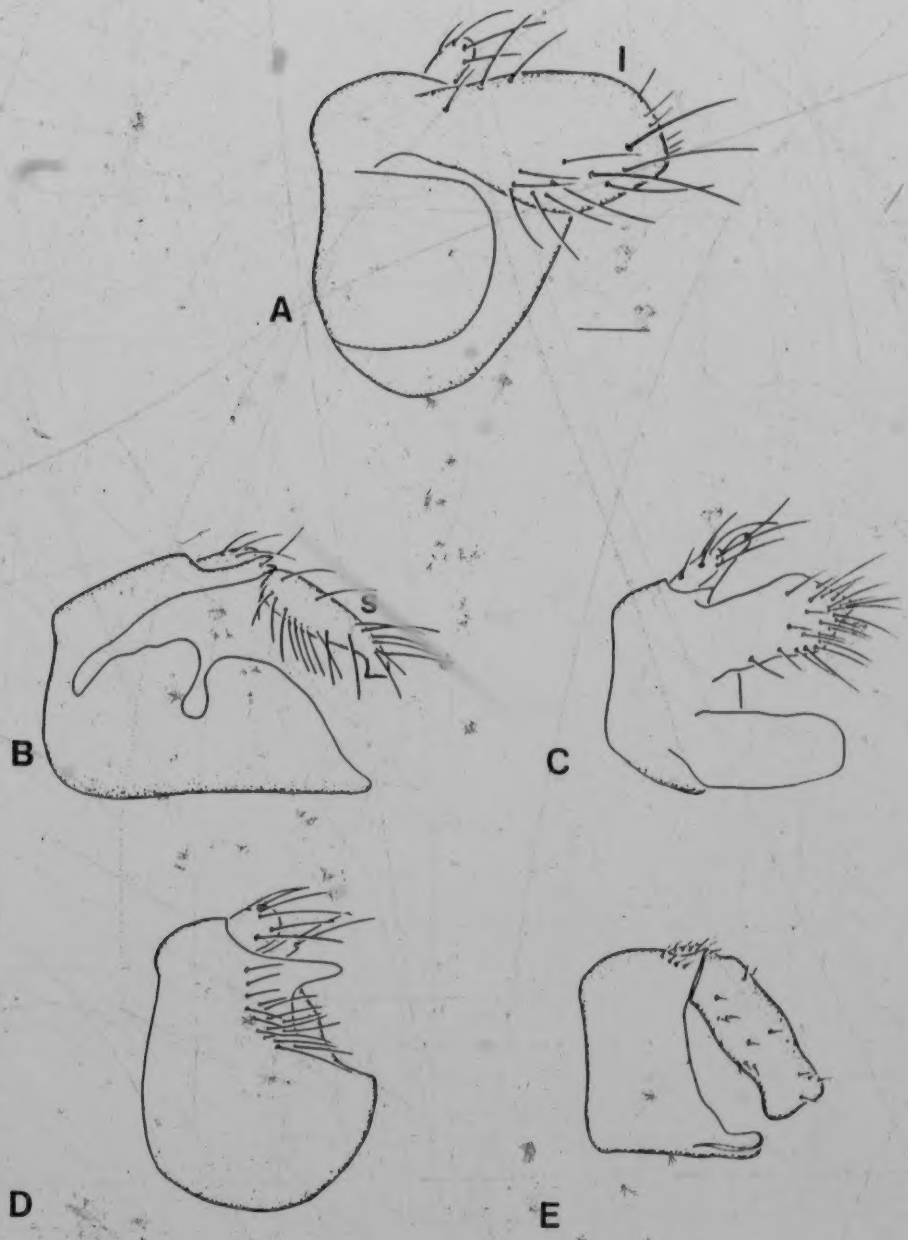

l
A
S
L
B
C
D
E

Fig. 5.3. Male terminalia, dorsal. A, *Chaetopleurophora pennsylvanica* (Malloch); B, *Chaetopleurophora* species D (Costa Rica); C, *C. erythronota* (Strobl); D, *C. multiseriata* (Aldrich); E, *C. semifurcata* (Borgmeier). Scale bar = 0.1mm, all figures to same scale. Abbreviations: l - left surstylus, s - subepandrial process.

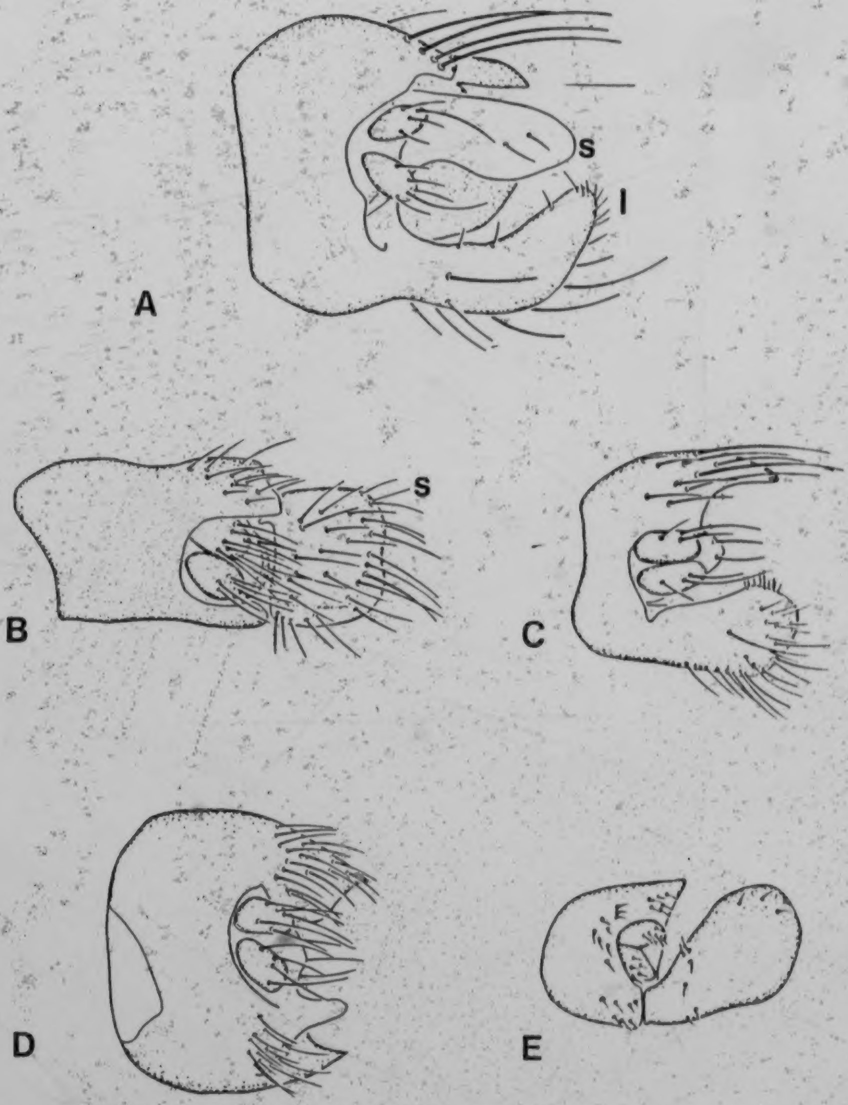

s
l
A
s
B
C
D
E

Fig. 5.4. Hypandria, ventral. A, *Chaetopleurophora pennsylvanica* (Malloch); B, *Chaetopleurophora* species D (Costa Rica); C, *C. erythronota* (Strobl); D, *C. multiseriata* (Aldrich); E, *C. semifurcata* (Borgmeier). Scale bar = 0.1mm, all figures to same scale. Abbreviations: l - left hypandrial process, r - right hypandrial process.

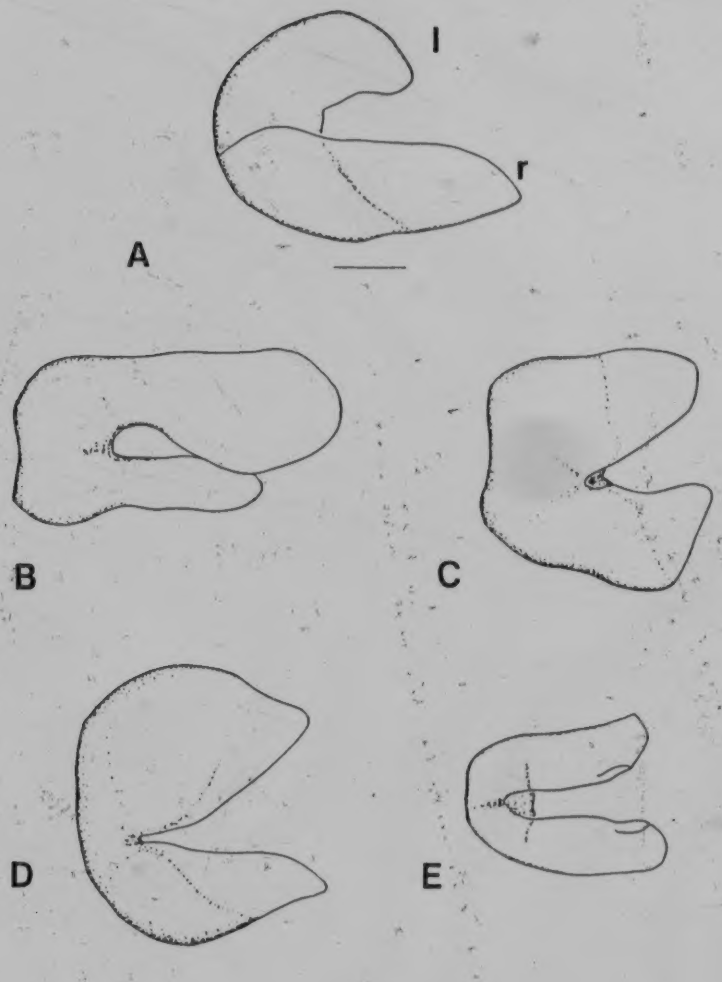

l
r
A
B
C
D
E

Fig. 5.5. A-D. Hypandria, ventral. A, *Spiniphora excisa* (Becker); B, *S. bergenstammi* (Mik); C, *Coniceromyia arizonensis* Borgmeier; D, *Anevrina spinipes* (Coquillett). E-F. Female terminalia, ventral. E, *S. excisa*; F, *C. eurythronota*. Scale bar = 0.1mm, all figures to same scale. Abbreviations: l - left hypandrial process, r - right hypandrial process, s7, s8 - sternite 7, sternite 8.

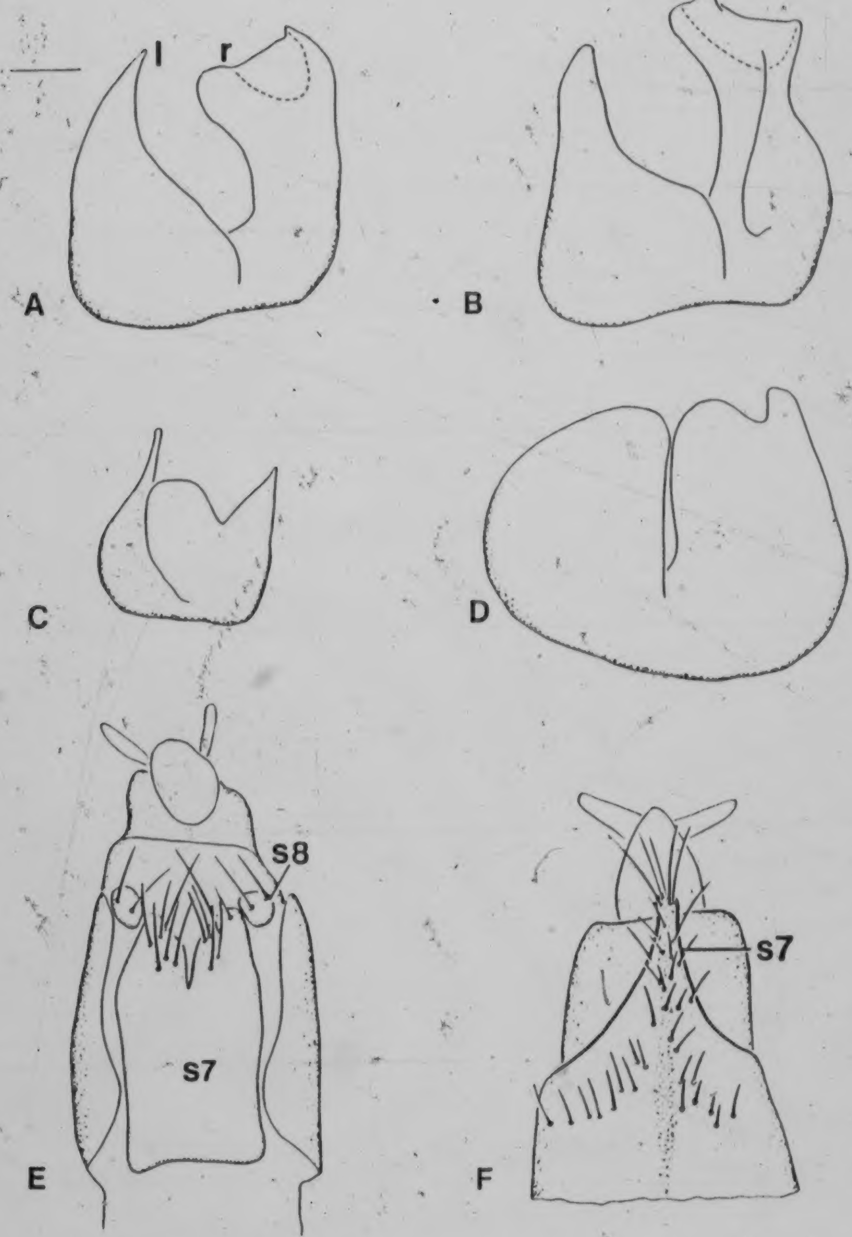
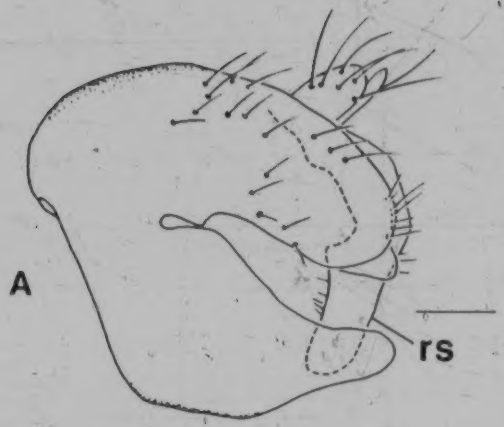
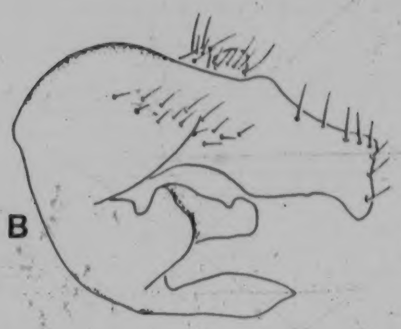

l
r
A
B
C
D
S8
s7
E
S7
F

Fig. 5.6. Male terminalia, left lateral. A, *Spiniphora excisa* (Becker); B, *Coniceromyia* sp. (Costa Rica); C, *Anevrina thoracica* (Meigen). Scale bar = 0.1mm, Figs. A-B to same scale. Abbreviation: rs - right surstylus.


A
rs


B

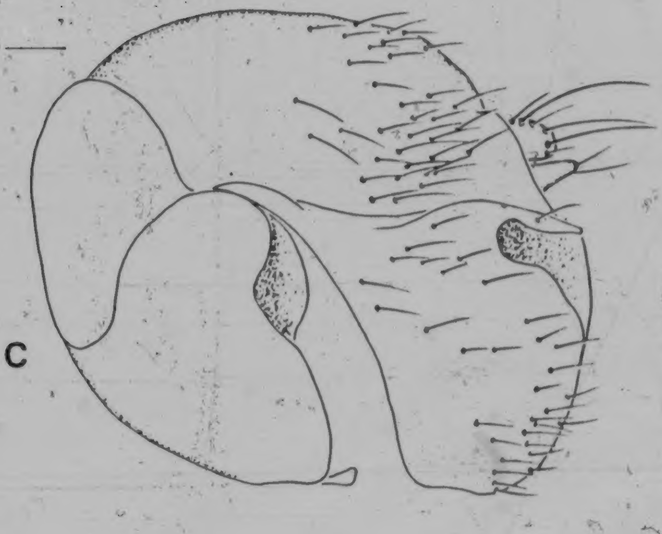
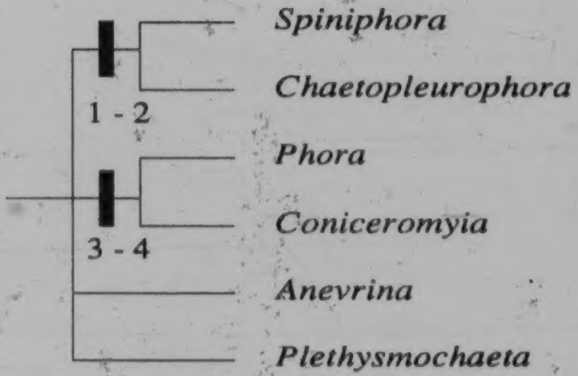

C

Fig. 5.7. Hypothesized relationships of the Phorinae.


Spiniphora
Chaetopleurophora
1 - 2
Phora
Coniceromyia
3 - 4
Anevrina
Plethysmochaeta

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4

6. REVISION AND PHYLOGENETIC CLASSIFICATION OF THE GENUS *AENIGMATIAS* MEINERT 1890 (TRIBE AENIGMATIINI), AND OF THE GENERA OF TRIBE DIPLONEVRINI (DIPTERA: PHORIDAE: AENIGMATIINAE)

6.1 Introduction

The genera *Diplonevra* Lioy and *Dohrniphora* Dahl are groups of relatively large and conspicuous phorid flies which, because of their widespread distribution and saprophagous lifestyle, are found in many general insect collections. The close relationship between the two is evident from previous classifications that united them into a single genus, *Diplonevra*. Although these flies were known long ago, their relationships, like those of other phorids, were not well understood. They are classified traditionally in the subfamily Phorinae, a paraphyletic group since organized into four monophyletic taxa (Chapter 3). The genera *Diplonevra* and *Dohrniphora* belong in a monophylum (named the Diplonevrini) with the Aenigmatiinae, a group of flies with limuloid females living in the nests of social insects (Chapter 3). Here, the other members of the Diplonevrini are identified, and the phylogenetic relationships of the group reconstructed.

6.2 Material and methods

Material was examined from the following collections, the names of which are preceded by a coden, used as an abbreviation for reference to these collections (names of curators in parentheses).

BVB - Collection of the author.

CNC - Canadian National Collection, Biosystematics Research Centre, Ottawa, Ontario, Canada (J.M. Cumming)

USNM - United States National Museum, Smithsonian Institution, Washington, DC, USA (F.C. Thompson)

ZFMK - Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (H.Ulrich)

Taxa from outside of the Nearctic Region frequently were used for comparison and to test hypotheses based on Nearctic specimens. Because of our limited knowledge about the Neotropical, Oriental, Australasian and Afrotropical phorid faunas, many of the species from these regions were not identified to species. This is in recognition of the incomplete coverage given by existing keys, as well as the realization that there are a great many undescribed species in regions outside of North America and Europe.

Full taxonomic synonymies are not given in this paper, except for those not found in Borgmeier (1968, 1971).

Male terminalia were examined by treatment in hot 10% KOH, and rinses of 30% acetic acid, water, and alcohol. They were then placed in an evaporating dish with a drop of glycerine and about 2ml of alcohol, and were put on a warming tray to allow the alcohol to evaporate off. Terminalia were then placed in glycerine jelly on glass slides and examined with light microscopy.

Some specimens were gold-coated and examined with a Cambridge 100 Scanning Electron Microscope.

Hypothesized relationships were reconstructed using standard cladistic techniques (Hennig, 1966). The cladogram in this paper was constructed manually, without computer algorithms. The data set was checked subsequently with the computer program Hennig-86 (Farris, 1989) to seek further equally parsimonious cladograms.

6.3 Terms

Recent reviews of Diptera phylogeny have postulated adelphotaxon (Griffiths, 1972), ancestor-descendant (Chvála, 1983) or no special relationship (McAlpine, 1989) between the Orthogenya and Cyclorrhapha. This disagreement affects the terms used to refer to the male genitalia, and I deal with it as I have previously (Brown, 1987).

The terms synapotypic, apotypic, plesiotypic etc. have been used in this paper as more general terms, rather than synapomorphic, apomorphic, plesiomorphic and so on that refer only to structure (Chapter 2, Terms). Other terms not used by Hennig, but subsequently proposed by Ax (1987) are used in this work: adelphotaxon (=sister-group) and groundpattern (=groundplan). The reasons for preferring the use of these more recent terms are those of Ax (1987).

6.4 Reconstructed Phylogeny of the Diplonevrini

The phylogeny of this group (depicted in Fig. 6.5), based on the character matrix in Table 6.1 was reconstructed using the following hypothesized, synapotypic character states:

1 Wing vein R_{2+3} absent.

The loss of this wing vein has occurred many times in the Phoridae, but it is still most parsimonious to consider its loss in *Multinevra* and *Hypocerides* as a synapotypy. Since this character state is subject to so much homoplasy, the adelphotaxon relationship it supports is extremely tenuous.

2 Enlarged setae present basally on hind femur of male (Fig. 6.1A).

Males of most outgroup taxa lack these enlarged setae. Males of *Multinevra* and *Hypocerides*, have small, thin setae in the same region of the femur.

3 Rectal papillae in separate pouch (Fig. 6.4).

The rectum of adults of *Diplonevra* and *Dohrniphora* are in a pouch, laterally attached to the rest of the digestive system. In adults of some species, there is a long stalk upon which the rectum is mounted.

This character state has evolved convergently in *Sciadocera rufomaculata* (Chapters 2, 3).

4 Larva with ventral, anteriorly crenulate sclerite (Kloter *et al.*, 1977, Figs. 6, 8, 11; Schmitz, 1949, Fig. 141.8).

5 Larva with thoracic tergites present (Kloter *et al.*, 1977; Schmitz, 1949).

6 Palpus two-segmented.

Most outgroup taxa (including *Aenigmatias*) have the palpus one-segmented (see also Chapter 3).

7 Anepisternum setulose (Fig. 6.1B).

This character state has evolved many times in the Phoridae, but based on outgroup evidence (Chapter 3), it is still considered a derived condition.

8 Wing vein R_s with long setae (Brues, 1930, Fig. 1b; Disney, 1987b, Fig. 2; Disney, 1990b, Fig. 4).

6.5 Classification

This classification depicts the relationships of the taxa using sequencing and subordination. Taxa equally indented are adelphotaxa; when there are more than one such group they are successive adelphotaxa, unless labelled *sedis mutabilis* (Wiley, 1981).

SUBFAMILY AENIGMATIINAE
- Tribe Aenigmatiini
  - *Aenigmatias* Meinert
- Tribe Diplonevrini
    - *Hypocerides*-group
        - *Hypocerides* Schmitz
        - *Multinevra* Disney

Diplonevra-group

Diplonevra Lioy

Dohriniphora-subgroup

Dohrniphora Dahl

Aenictomyia Brues *sedis mutabilis*

Dicranopteron Schmitz *sedis mutabilis*

Myopiomyia Disney *sedis mutabilis*

6.6 Revision of genera

SUBFAMILY AENIGMATIINAE SCHMITZ 1926

Platyphorinae Enderlein 1908, Schmitz 1915

Type genus: *Aenigmatias* Meinert 1890 (original designation)

Diagnosis. Female with lateral sclerites on abdominal segment 7. Hind tibia with at least one, and in some species many, rows of enlarged setulae (Figs. 6.1C-D). Wing veins R_{2+3} and R_{4+5} subparallel (Chapter 3, Fig. 3.4F; Schmitz, 1949, Figs. 70-72).

Geographic distribution. The members of the tribe Aenigmatiini (see below) are found world-wide, although there is only one described genus each in the Nearctic and Neotropical Regions (Brown, submitted). Three genera of Diplonevrini are in all biogeographic regions, while the other three are in the Oriental and Afrotropical Regions. Only the genera *Diplonevra* Lioy and *Dohrniphora* Dahl are distributed widely with many described species.

Phylogenetic Relationships. The exact relationships of this subfamily are not known. They are part of an unresolved trichotomy, also involving the subfamilies Conicerinae and Metopininae (Chapter 3).

Included Nearctic Region Taxa. Tribe Aenigmatiini, tribe Diplonevrini (Chapter 3).

Tribe Aenigmatiini Schmitz

Type genus: *Aenigmatias* Meinert 1890

Diagnosis. Prothoracic spiracle dorsal, with lateral borders of scutum below. Female of most species depressed, limuloid, with setation of frons, legs and body reduced or absent; wing of female reduced or absent.

Way of life. The species for which life history information is available are termitophilous or myrmecophilous (Kistner, 1982).

Geographical distribution. Most genera of these flies occur in the Old World tropics. One genus, however, lives in the Holarctic Region (*Aenigmatias*) and one lives in the

Neotropical Region (*Cyrtophorina* Borgmeier and Prado). So far, there are no records of this taxon from Australia.

Phylogenetic relationships. This group is the adelphotaxon of the tribe Diplonevrini (see below).

Within the Aenigmatiini, the relationships are not well founded and, since most of these taxa occur outside of the Nearctic Region (the area this revision originally intended to cover), the question of their relationships are not considered further.

Known fossil material. Protoplatyphora tertiaria Brues (from Baltic amber) is a member of the Aenigmatiini that bears some primitive characters, as discussed by Brues (1939). These character states, namely presence of setae on the frons and scutellum, indicated to him a transitional form between living *Aenigmatias* and other phorids, but the structure of the extant species *Synaptophora critica* Brown (Chapter 3) is relatively much more primitive. The presence of several longitudinal rows of enlarged setulae on the hind tibia of the specimen of *Protoplatyphora* may be a synapotypic character state linking this genus with *Aenigmatias*, and, since it appears to exhibit no autapotypic character states relative to *Aenigmatias*, I doubt that it merits separate generic status.

Included Nearctic Region taxa. Aenigmatias Meinert.

Taxa from other biogeographic regions. Aenigmatistes Shelford (Africa), *Aenigmatopoeus* Schmitz (Africa), *Assmutherium* Schmitz (India), *Cyrtophorina* Borgmeier and Prado (South America), *Epicnemis* Borgmeier (Southeast Asia), *Euryophora* Schmitz (Madagascar), *Euryplatea* Schmitz (Africa), *Microplatyphora* Schmitz (Africa), *Misotermes* Schmitz (Southeast Asia), *Psyllomyia* Loew (Africa), and *Synaptophora* Brown (Africa). The Neotropical Region genera *Borgmeieriphora* Prado, *Colyeria* Borgmeier and Prado, *Melittophora* Brues, and *Platydipteron* Borgmeier and Prado, all formerly placed in the Aenigmatiinae (=Aenigmatiini) belong in the Metopininae (Brown, submitted).

6.6.1 *Aenigmatias* Meinert 1890

(Fig. 6.1D)

Type species: *Aenigmatias blattoides* Meinert 1890 = *Platyphora lubbocki* Verrall 1877 (monotypy).

Derivation of generic name. Presumably, this name refers to the enigmatic appearance of adult females of this genus.

Diagnosis. The only Aenigmatiini found in the Nearctic Region. Female apterous, limuloid. Male fully winged; terminalia with large surstyli.

Way of life and immature stages. The species of this genus are myrmecophilous, and one species was reported as a pupal parasite of ants of the genus *Formica* (Donisthorpe, 1927).

There are no descriptions of immature stages.

Collecting methods. Adult males, and sometimes associated females, are collected by Malaise traps.

Geographical distribution. Holarctic Region.

Phylogenetic relationships. Unknown. The phylogeny of Aenigmatiini needs to be studied. The structure of the male terminalia of males of *Aenigmatias* is relatively primitive, as surstyli similar to those of male phorines are present.

Hypothesized autapotypic character states of *Aenigmatias* include the following:

1 Hind tibia with several rows of enlarged setulae.

Number of recognized species. Total of thirteen; six are in the Nearctic Region.

Material examined. I examined material of all six Nearctic Region species of this genus; localities are listed in Brown (submitted). Fifteen other specimens from Alberta, Arizona, British Columbia, California and Ontario were examined also, but could not be placed to species. This genus, like most other phorid genera, needs species level revision.

Tribe Diplonevrini Enderlein 1924

Type genus: *Diplonevra* Lioy 1864 (original designation).

Notes about synonymy. Enderlein suggested this name for those phorids with wing vein R_{2+3} present, and at least the middle tibia with one or more large setae. Its present, more restricted definition is outlined below.

Diagnosis. Male with differentiated sclerite (=epandrial ring, segment 10 of Disney, 1986) between epandrium and cercus (Figs. 6.2A-F, 6.3A-F).

Geographical distribution. World-wide.

Phylogenetic relationships. This tribe is the adelphotaxon of the Aenigmatiini.

The relationship between *Diplonevra* and *Dohrniphora* has been recognized for a long time, and at one time they were considered to be subgenera in the same genus, *Diplonevra*. Similarly, *Aenictomyia* and *Apopteromyia* Beyer also were considered subgenera of *Diplonevra*, and when describing *Myopiomyia* and *Multinevra*, Disney realized that both belonged in a group with *Diplonevra*.

Known fossil material. Several species of *Diplonevra* have been described from Baltic amber (Borgmeier, 1968), whereas many specimens of *Dohrniphora* are found in Dominican amber (personal observation). Only one species of *Dohrniphora* was described from Dominican amber (Disney, 1987a), a description that unfortunately was made without due caution. This species, *Dohrniphora poinari*, is known only from the holotype female, which Disney himself (1987a, pg. 377) and other phorid workers would not describe if it were a specimen of an extant species. Disney justified this description by stating that:

> "In the case of fossils more than 10 m.y.B.P in age this precaution can be safely ignored; although there remains a low probability of a male of one of these species being discovered and, because of sexual dimorphism, treated as a distinct species in error."
>
> (Disney, 1987a)

This justification, however, is on shaky ground, when one considers the large number of specimens of *Dohrniphora* in Dominican amber. An example is my small collection that contains twenty-six pieces of Dominican amber; of these, three contain specimens of *Dohrniphora*, including one that conceivably could be the male of *D. poinari*. Another factor to consider is the age of Dominican amber, some of which is much younger than the Oligocene dates given for the amber from some mines. Indeed, some of this so-called amber may be much younger, and corresponding males of *D. poinari* may still be extant. Certainly there are candidates in the living fauna of Costa Rica (personal observation). Without giving information on which amber mine these specimens were acquired from, it is impossible to tell how old they may be.

A further species of *Diplonevra* was described from a Pliocene compression fossil (Durrenfeldt, 1968), but the venation is atypical for this genus, and I am skeptical that it is classified correctly.

Included Nearctic Region taxa. ***Diplonevra*** Lioy, ***Dohrniphora*** Dahl, ***Hypocerides*** Schmitz.

Taxa from other biogeographic regions. ***Aenictomyia*** Brues (Philippines), ***Dicranopteron*** Schmitz (Java), ***Multinevra*** Disney (Africa), ***Myopiomyia*** Disney (Sulawesi).

***Hypocerides*-group**

Diagnosis. Wing vein R_{2+3} absent.

6.6.2 ***Hypocerides* Schmitz 1915**

(Fig. 6.2D)

Type species: *Hypocera difformis* Brues 1905 (by original designation)

Derivation of generic name. Named for the supposed similarity between this genus and *Hypocera* Lioy.

Diagnosis. Wing with costa enlarged between veins R_1 and R_{4+5}; vein R_{2+3} absent.

Description. Sensory setae present on hind femur (in *H. aethereus*). Ring of epandrium incompletely developed, represented by lateral indentation only (Fig. 6.2D). Female lacking lateral sclerites on terminalia.

Way of life and immature stages. Unknown.

Collecting methods. I have not collected individuals of this genus.

Geographical distribution. Australasian, Afrotropical, Neotropical and Nearctic Regions.

Phylogenetic relationships. This genus is considered tentatively the adelphotaxon of *Multinevra* (see below). Unfortunately, I could not see some important characters in the air-dried specimens available to me.

Hypothesized autapotypic character states of *Hypocerides* includes the following:

1 Costa enlarged between wing veins R_1 and R_{4+5} (see Borgmeier, 1966, Fig. 102).

Number of recognized species: Total of eight; one is found in the Nearctic Region.

Nearctic Region material examined: ***H. nearcticus* Borgmeier**, holotype ♂, USA: Virginia: Fairfax Co., Falls Church, 20.vi.1952, W.W.Wirth (USNM).

Material examined from other zoogeographic regions. ***H. aethereus* Schmitz**, 1♂, 1♀ paratype, KENYA: Kisumu, v.1935, C.B.Symes, "in aeroplane" (ZFMK); ***H. paranenis*** Borgmeier, 1 ♂, BRAZIL: Parana, Rio Negro, 1.i.1925, F.M.Witte (ZFMK).

6.6.3 ***Multinevra* Disney 1979a**

Type species: *Multinevra macropygidia* Disney 1979a (original designation).

Derivation of generic name. "*Multinevra* refers to the multiple palisade rows of hairs on the hind tibia, in contrast to the double row typical of *Diplonevra*" (Disney, 1979a).

Diagnosis. Only male known. Palpus one-segmented. Anepisternum bare. Wing vein R_{2+3} absent. Hind tibia with numerous (6-7 in type species) dorsal, longitudinal setal rows. Hypandrium with anteroventral, spinose process.

Way of life and immature stages. Unknown

Geographical distribution. Africa, Nepal, Thailand.

Phylogenetic relationships. This genus is considered the adelphotaxon of *Hypocerides*, although the evidence for this arrangement is extremely tenuous.

I have examined three undescribed species of *Multinevra*, all of which bear the distinguishing characters of this group, as outlined in the original description. Additionally, these flies exhibit anteroventral, spinose hypandrial processes that were not reported by Disney (1979a). Unfortunately, the females of all species are unknown.

Hypothesized autapotypic character states of *Multinevra* include the following:

1 Cercus and hypoproct elongate.

2 Hypandrium with anteroventral, spinose process.

3 Hind tibia with several rows of enlarged setulae.

Number of recognized species. One, the type species.

Material examined. ***Multinevra* sp.1**, 12♂, NIGERIA: Ibadan, 8.vii.-7.xii.1962, D. Eidt, Malaise trap (BVB, CNC); ***Multinevra* sp.2**, 7♂, NEPAL: Kathmandu, Godavari, 6000', 15.vii.-17.viii.1967, Canadian Nepal Expedition (BVB, CNC); ***Multinevra* sp.3**, 1♂, THAILAND: 70km SW Chiang Mai, Doi Inthanon National Park, 2470m, 31.i.-7.ii.1989, T.W.Thormin, Malaise trap (BVB).

***Diplonevra*-group**

Diagnosis. Palpus two-segmented. Enlarged setae present basally on hind femur of male (Fig. 6.1A). Rectal papillae in separate pouch (Fig. 6.4). Larva with ventral, anteriorly crenulate sclerite (Kloter *et al.*, 1977, Figs. 6, 8, 11; Schmitz, 1949, Fig. 141.8) and thoracic tergites present (Kloter *et al.*, 1977; Schmitz, 1949).

Diplonevra Lioy 1864

Apoptermyia Beyer **new synonymy**

(Figs. 6.1C, 6.2F, 6.3A-F)

Type species: *Bibio florea* Fabricius 1794 (designated by Enderlein, 1924)

Derivation of generic name. Literally translated, this name means "two-nerved" and refers to the bifurcate "marginal vein" (*nervatura marginale*), presumably R_{2+3} and R_{4+5}. This name was no doubt intended to be "*Diploneura*" (based on the Greek *neuron* for nerve), but the habit of writing Latin words with Roman conventions (such as "v"s instead of "u"s), led to the name *Diplonevra*.

Notes about synonymy. The subgenus *Apopteromyia* was proposed by Beyer (1958) for the unusual termitophilous species *Diplonevra gynaptera* Fuller and Lee (1938). Later, Borgmeier (1967) raised the rank of this taxon to genus, an opinion that Disney (1990a) disregarded in his taxonomic treatment of Australasian and Oriental

Diplonevra. Based on re-examination of a male and female specimen of *A. gynaptera*, it is clear that this taxon should be combined with *Diplonevra* and the names synonymized (**new synonymy**). Based on the existing evidence, it should not be considered a valid subgenus. The length of the stalk of the cercus in the male terminalia of *Diplonevra* species forms a convincing transformation series, and the stalk of *D. gynaptera* (Fig. 6.3F) clearly is intermediate in length between that of males of some relatively primitive (Figs. 6.2F, 6.3A) and derived (Figs. 6.3D-E) *Diplonevra* species. Therefore *D. gynaptera* is more closely related to some *Diplonevra* species than others, and it belongs within this genus.

Diagnosis. Wing vein R2+3 present. Hind tibia with two longitudinal, dorsal rows of enlarged setulae (Fig. 6.1C). Cerci mounted on short to long epandrial stalk (long in all Nearctic Region species) (Figs. 6.2F, 6.3A-F).

Way of life and immature stages. Adults of *Diplonevra* species have been reared from a number of decaying media, such as dead locusts, dead caterpillars, wasp nests, injured earthworms, fungi, and digested sewage sludge (all cited in Ferrar, 1987). Earthworms, in particular, are mentioned repeatedly as hosts for these flies, and records exist for *D. nitidula* (Meigen) (Disney, 1979b) and *D. pilosella* Schmitz (Colyer, 1950) having been attracted to or breeding in them. Many adult female specimens of *D. nitidula* were collected Manitoba, Canada, by baiting a pitfall trap with dead earthworms, and an earthworm left on a fishing hook overnight was covered with females the next day (D.A. Pollock, personal communication).

Disney (1985, 1986) reported on a much more specialized lifestyle in *D. mortimeri* Disney and *D. watsoni* Disney, both of which occur in Sulawesi. The flies were attracted to exposures of several species of termites, caused by disturbing the termite colonies. Adult females of these flies apparently lure worker termites away from their nests, somehow subdue them, and lay a single egg. The female then guards the termite for an unknown period of time.

Larvae of this genus are distinctive and extremely similar to those of *Dohrniphora* (Schmitz, 1949, Figs. 141-142; Kaneko,K & Furukawa, 1977). The puparium of *D. pilosella* Schmitz was described by Colyer (1950), and that of *D. armipes* (Brues) was described by Schmitz (1940). The larva and puparium of *D. gynaptera* were described by Fuller and Lee (1938).

Collecting methods. These flies often are collected in Malaise traps, pan and flight-intercept-traps. Adults of *D. nitidula* are attracted to birch sap (J.R. Vockeroth, personal communication) and dead earthworms.

Geographical distribution. Found worldwide.

Phylogenetic relationships. This genus is the adelphotaxon of the *Dohrniphora*-subgroup.

Hypothesized autapotypic character states of *Diplonevra* include the following:

1 Hind tibia with 2 or more rows of enlarged setulae.

This character state offers only tenuous evidence for the monophyly of this genus; however, I am reasonably convinced that this is a monophyletic group. A single dorsal row of enlarged setulae is probably the primitive state for this subfamily, and is found in adults of *Synaptophora*, *Misotermes*, *Epicnemis*, *Cyrtophorina* (all Aenigmatiini) *Hypocerides*, and *Dohrniphora*-group species. More than one row are found in adults of *Aenigmatias*, *Aenigmatistes* (both Aenigmatiini), *Multinevra* and *Diplonevra*. There is no such row on the hind tibiae of males of *Euryphora*.

The presence of a short cercus mounted on a long stalk was considered formerly a suitable defining character state of *Diplonevra*, but males of some relatively primitive species from Australia and the Oriental Region have male terminalia at a similar stage of modification as males of the relatively primitive genus *Hypocerides* (compare Figs. 6.2D, 6.3C).

Number of recognized species: Total of seventy-three; five are found in the Nearctic Region.

Nearctic Region material examined. ***D. funebris*** **(Meigen)**, 1♂, CANADA: Ontario: Guelph, South Arboretum, 19-24.vi.1985, B.V.Brown, Malaise trap, deciduous forest (BVB), 1♂, Stouffville, 8-22.vi.1985, B.V.Brown, Malaise trap (BVB); ***D. gaudialis*** **(Cockerell)**, 4♂, USA: Arizona: Cochise Co., near Portal, S.W.R.S., 18.vii, 22.vii, 14.viii, 25.viii.1965, V.Roth, Malaise trap (BVB), 1♀, 9-10.vi.1986, B.V.Brown, Malaise trap (BVB), 1♂, 18.5km W. Portal, Basin Trail head, 7-10.vi.1986, B.V.Brown, Malaise trap, 1950m, oak/ pine/ juniper (BVB); 24♂, 7♀, California: Tuolumne Co., 1.5km E. Tuolumne, 750m, 15-26.vi.1986, B.V.Brown and T.G.Spanton, Malaise trap, carrion trap, oak foothill forest (BVB), 2♂, 1♀, 6km E. Tuolumne, River Ranch Campground, 22-26.vi.1986, B.V.Brown, malaise trap, oak forest/ field, 750m (BVB); ***D. nitidula* (Meigen)**, many males and females, collected from May to October, from the following localities: CANADA: Ontario: Footes Bay, Guelph, Ottawa, Stouffville; also *circa* 50 specimens, CANADA: Manitoba: Winnipeg, 5-6.viii.1990, D.A. Pollock, ex dead lumbricid (BVB).

Material examined from other zoogeographic regions. ***D. alleni* Brues**, 10♂ and 4♀, WEST INDIES: St. Kitts, Greenhill, 300m, 12-31.vii., 1-27.viii.1985, L.D.Coote, Malaise trap, rain forest (BVB); ***D. gynaptera* Fuller & Lee**, 1♂, 1♀ paratype, AUSTRALIA: Sydney, 1935, nests of *Eutermes* (ZFMK); ***D. predicta* Disney**, 1♂, AUSTRALIA: New South Wales, Monga State Forest, 19-24.i.1984, L.Masner (BVB); ***Diplonevra* sp.2**, 3♂, ECUADOR: Napo, Quito-Baeza Road, 4000m, L.Masner, elfin forest (BVB); ***Diplonevra* sp.3**, 1♂, VENEZUELA: Merida, South of Bolivar National Park, La Aguada, 13.v.1981, 3000m, L.Masner (BVB); ***Diplonevra* sp.4**, 1♂, VENEZUELA: Lara, Yacambu, 1200m, 7.v.1981, H.Townes, cloud forest, Malaise trap (BVB); ***Diplonevra* sp. 5**, 1♂, CHILE: Chiloe, Ahori Alto, 70m, iv.1988, primary forest, Malaise trap, L.E.Peña (BVB); ***Diplonevra* sp. 6**, 2♀, COSTA RICA: San Jose, 16km S. Empalme, 2600m, iii-iv. 1989, P.Hanson & I. Gauld, Malaise trap (BVB);

***Diplonevra* sp. 7** (sp.A), 1♂, AUSTRALIA: Tas. Mt. Field N.P., 8-14.i.1984, L.Masner, Malaise trap (BVB); ***Diplonevra* sp. 8** (sp.B), 1♂, AUSTRALIA: Tas. Mt. Field N.P., 8-14.i.1984, L.Masner, Malaise trap (BVB); ***Diplonevra* sp. 9** (sp.C), 1♂, AUSTRALIA: New South Wales, Monga State Forest, 19-24.i.1984, L.Masner (BVB); ***Diplonevra* sp. 10** (sp.E), 1♂, AUSTRALIA: New South Wales, Monga State Forest, 19-24.i.1984, L.Masner (BVB); ***Diplonevra* sp. 11**, MADAGASCAR: Fianarantosoa, 7km W Ranomafana, 1100m, 1♀, 22-31.x.1988, W.E. Steiner, small clearing in montane forest (BVB); ***Diplonevra* sp. 12** (sp.F), 1♂, AUSTRALIA: Queensland, Mt. Lewis Road, 1000m, 17-24.ii.1984, L.Masner, Malaise trap (BVB).

Dohrniphora-subgroup

Diagnosis. Anepisternum setulose (Fig. 6.1B).

6.6.5 *Dohrniphora* Dahl 1898

(Figs. 6.1A-B, 6.2E)

Type species: *Dohrniphora dohrni* Dahl 1898 (original designation).

Diagnosis. Hind tibia with one row of enlarged setulae. Wing without enlarged setae. Male epandrial ring reduced dorsally (Fig. 6.2E).

Derivation of generic name. It is not clear for whom this genus was named. Musgrave (1932) listed three Dohrns from Stettin, Germany: Carl August Dohrn (1806-1892) and his two sons Felix Anton Dohrn (1840-1909) and Heinrich Dohrn (1838-1913). The original description by Dahl (1898) did not specify which of these men was being honored.

Way of life and immature stages. Life history information on *D. cornuta* is given by Kloter *et al.* (1977).

The larva and pupa of *D. cornuta* have been described by Kloter *et al.* (1977) and Kaneko and Furukawa (1977).

Collecting methods. These flies are encountered frequently in Malaise and carrion trap residues. At La Selva, Costa Rica, hundreds of adult females were attracted to dead termites when a colony was broken open.

Geographical distribution. Found world-wide.

Phylogenetic relationships. This genus is the adelphotaxon of *Aenictomyia* + *Myopiomyia* + *Dicranopteron* (see below).

This is a distinctive genus, with few differences in structure of male terminalia of different species. Hypothesized autapotypic character states of *Dohrniphora* cannot be proposed at this time, until the males of *Aenictomyia*, *Dicranopteron* and *Myopiomyia* are collected and the entire group revised.

Number of recognized species. Total of one hundred and ten; six have been found in the Nearctic Region.

Nearctic Region material examined. ***D. cornuta*** **(Bigot)**, 1♂, CANADA: Ontario: Stouffville, 14-20.viii.1983, B.V.Brown, Malaise pans (BVB), 10♂, USA: Arizona: Cochise Co., near Portal, S.W.R.S., 24.vii-17.ix.1965, V.Roth, Malaise trap (BVB), 1♀, Pima Co., N. of Tucson, General Hitchcock Campground, 21.viii.1984, B.V.Brown, low plants (BVB), 14♂, WEST INDIES: Nevis: Newcastle, 9.vii-3.viii.1984, B.Buckland, pan trap (BVB), St. Kitts: Basseterre, 16-30.vi.1985, L.D.Coote, pan trap, coastal (BVB), ***D. incisuralis*** **(Loew)**, 17♂, 9♀, CANADA: Ontario: Guelph, South Arboretum, vi-ix.1984, 1985, B.V.Brown, Malaise trap, intercept trap (BVB), 4♂, 1♀, Footes Bay, shore of Lake Joseph, 28.vii-9.viii, 11-30.viii, 30.viii-15.ix.1985, B.V.Brown, Malaise trap, second growth deciduous forest (BVB), ***D. perplexa*** **(Brues)**, 2♀, CANADA: Ontario: Guelph, South Arboretum, 4-7.vii.1984, B.V.Brown, Malaise trap, deciduous forest (BVB), USA: Arizona: 4♀, Cochise Co., Coronado National Memorial, 11-15.viii.1984, B.V.Brown, carrion trap (BVB), 1♀, near Portal, S.W.R.S., 8.viii.1965, V.Roth, Malaise trap (BVB), 2♂, FLORIDA: Highlands Co., Lake Placid, Archbold Biological Station, 30.xii.1985, B.V.Brown, Malaise trap, hammock forest (BVB).

Material examined from other zoogeographic regions. **D. ecitophila**, 26♀, ECUADOR: Pichincha: 47km S. Santo Domingo, Rio Palenque Science Center, 1-3.v.1987, B.V.Brown, *Eciton burchelli* bivouac, 180m rain forest (BVB); **D. gigantea (Enderlein)**, 8♂, 1♀, VENEZUELA: Lara, Yacambu, 7.v.1981, H.Townes, Malaise trap, cloud forest (BVB), 3♂, 8♀, ECUADOR: Pichincha, above Tinalandia, 7.v.1987, 1250m, B.V.Brown, ravine, wet montane forest (BVB), 1♀, Tinalandia, 6-13.vi.1987, B.V.Brown, 710m, clubhouse windows (BVB), ***Dohrniphora* sp.1**, 1♂, UGANDA: Entebbe, 17.xi.1972, H.Falke, lake shore, 3720' (BVB), ***Dohrniphora* sp.2**, 1♂, ECUADOR: Pichincha, 47 km S. Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown & L.Coote, Malaise trap, rain forest, 180m (BVB), ***Dohrniphora* spp. 3-12**, many male specimens, COSTA RICA: Heredia, La Selva Biological Station, 40m, 23-26.v.1988, B.V.Brown, Malaise trap, primary rain forest, SSO 50 (BVB).

6.6.6 *Aenictomyia* Brues 1930

Type species: *Aeneictomyia chapmani* Brues 1930 (by monotypy).

Derivation of generic name. Named for the ant genus *Aenictus* Shuckard, with which these flies were collected.

Notes about synonymy. This genus was elevated from the status of a subgenus by

Borgmeier (1967), who states that since both *Diplonevra* and *Dohrniphora* were being considered separate genera, *Aenictomyia* also deserved this rank. It is likely, however, that this genus is merely a markedly divergent species of *Dohrniphora*.

Diagnosis. Only female known. Anepisternum setulose dorsally; scutum with long setae; hind tibia with single dorsal, longitudinal setal row; single, long (*ca*. one-third wing length) seta at base of R_s. Disney (1990b) stated that the female of this genus has one-segmented palpi, but this needs confirmation by re-examining the type specimens.

Way of life and immature stages. Collected in the emigration columns of *Aenictus martini* Forel (name now a synonym of *A. gracilis* Emery; Wilson, 1964), running among the ants.

The immature stages are unknown.

Geographical distribution. Known only from the type series, collected in the Philippines.

Phylogenetic relationships. This genus forms a monophylum with *Dicranopteron* and *Myopiomyia*. The differences between *Myopiomyia* and *Aenictomyia* are so slight that they could be considered congeneric. Discovery of males of both of these genera would be useful.

Hypothesized autapotypic character states of *Aenictomyia* include the following:

1 Scutum with elongate setae.

2 Mid tibia with greatly elongate basal setae.

3 Costal setae greatly elongate.

Number of recognized species. One, the type species.

Material examined. None.

6.6.7 *Dicranopteron* Schmitz 1931

Type species: *Dicranopteron philotermes* Schmitz (original designation)

Derivation of generic name. This name is derived from the Greek *dikranon*, meaning pitchfork and referring to the enlarged fork of the radial wing veins.

Diagnosis. Lateral sclerites present laterally on segments 7 and 8. Frontal setae and wing reduced. Distal segment of palpus enlarged. Fork of wing vein R_s enlarged (Disney, 1990b, Figs. 4a-e). Hind tibia without rows of dorsal, enlarged setulae.

Way of life. All specimens have been found in termite nests, and at least one species is a parasitoid of termites (Disney, 1990b).

Immature stages. Unknown.

Geographical distribution. Oriental Region.

Phylogenetic relationships. This genus is related to *Aenictomyia* and *Myopiomyia.*

Some hypothesized autapotypic character states of *Dicranopteron* were given by Disney and Kistner (1990b), and I agree with all but the following: clypeus enlarged; labrum elongated, palpus two-segmented. All of these states are found in other diplonevrines.

Number of recognized species. Five.

Material examined. ***D. philotermes*** **Schmitz**, holotype ♀, JAVA (ZFMK).

6.6.8 *Myopiomyia* Disney 1987b

Type species: *Myopiomyia harmani* Disney 1987b (original designation).

Derivation of generic name. Named for the ant host, *Myopias* Roger (= *Pachycondyla* Smith; Snelling, 1981).

Diagnosis. Only female known. Similar to *Aenictomyia*, except wing veins R_s, M_1, M_2

and CuA_1 each with several long setae. Lateral sclerites present on segment 7 and 8.

Way of life and immature stages. Collected from nests of *Myopias* (=*Pachycondyla*) *maligna* (Smith).

The immature stages are unknown.

Geographical distribution. Sulawesi.

Phylogenetic relationships. This genus may be the adelphotaxon of *Aenictomyia*. The two are so similar that they could be considered congeneric.

Hypothesized autapotypic character states of *Myopiomyia* include the following:

1 Wing veins R_s, M_1, M_2 and CuA_1 with long setae.

Number of recognized species. One, the type species.

Material examined. None.

6.7 Conclusions and suggested future work

The reconstructed phylogeny of the Diplonevrini at present is based on inadequate information. Both sexes are known only for three of the seven currently recognized genera, but based on the material now available, some predictions about character states are made. The hindgut of adult *Aenictomyia*, *Dicranopteron* and *Myopiomyia* probably has the rectum separated from the rest of the gut by a short or long stalk. The larvae of these three genera likely all have the same structure as those of *Diplonevra* and *Dohrniphora*, with distinctive thoracic sclerites. Discovery of male specimens of *Aenictomyia*, *Dicranopteron* and *Myopiomyia*, females of *Multinevra*, and larvae of all genera is necessary before further progress will be made on this group.

6.8 Acknowledgements

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Table 6.1. Distribution of plesiotypic and synapotypic character states among the Diplonevrini. 0 - plesiotypic, 1 - synapotypic, ? - equivocal or unknown.

Character states	12345678
Taxa	
Hypocerides	10????00
Multinevra	1000?000
Diplonevra	01111100
Dohrniphora	01111110
Aenictomyia	0?????11
Dicranopteron	0????111
Myopiomyia	0????111

Fig. 6.1. A-B. *Dohrniphora* sp., male. A, posterior face of base of hind femur; B, thorax, lateral. C, *Diplonevra* sp., hind tibia, dorsal. D, *Aenigmatias curvinervis* Borgmeier, male, hind tibia, dorsal. Abbreviations: as - anepisternal setulae, s - enlarged setae of hind femur.

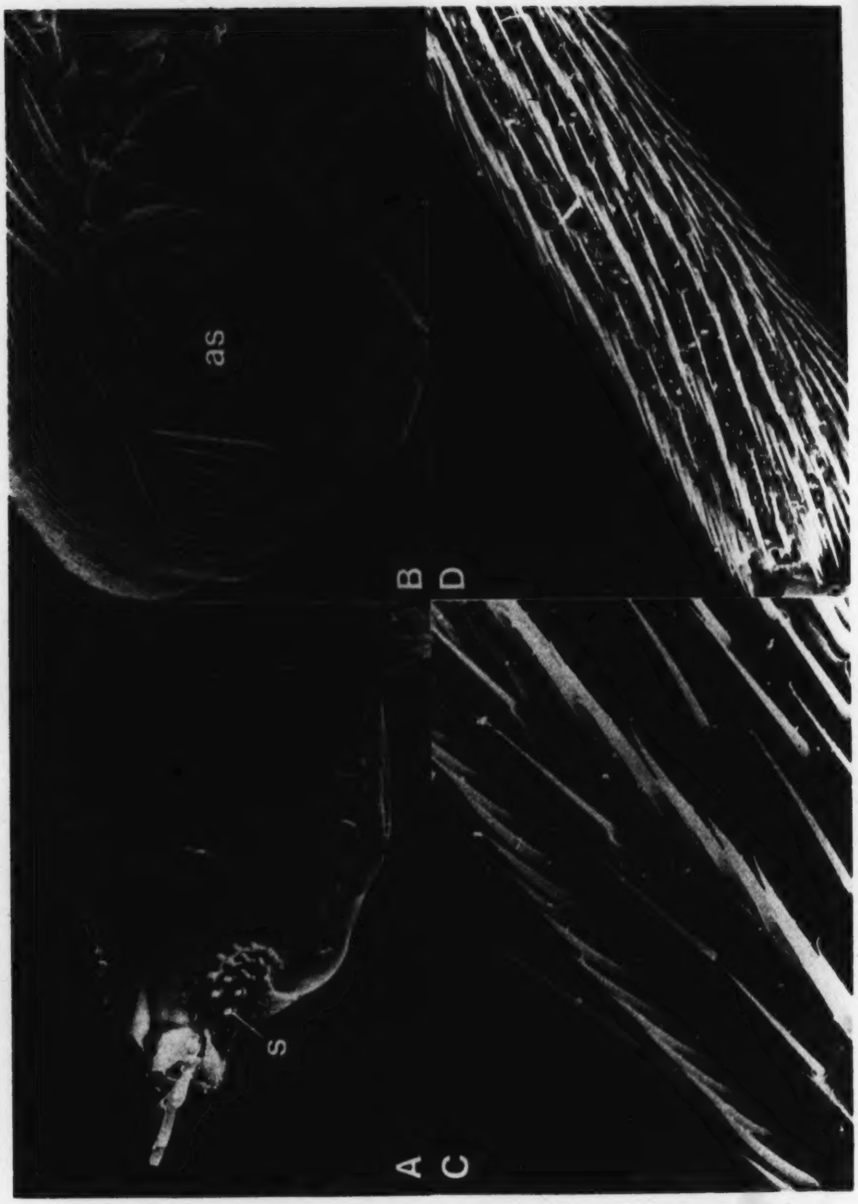

A
B
C
D
as
s

Fig. 6.2. A-F. Male terminalia, left lateral. A, *Multinevra* sp.; B, *Multinevra* sp.; C, *Multinevra* sp.; D, *Hypocerides aetherus* Schmitz; E, *Dohrniphora gigantea* (Enderlein); *Diplonevra* species 8. Scale bars = 0.1mm, all figures except D to same scale. Arrows indicate epandrial ring.

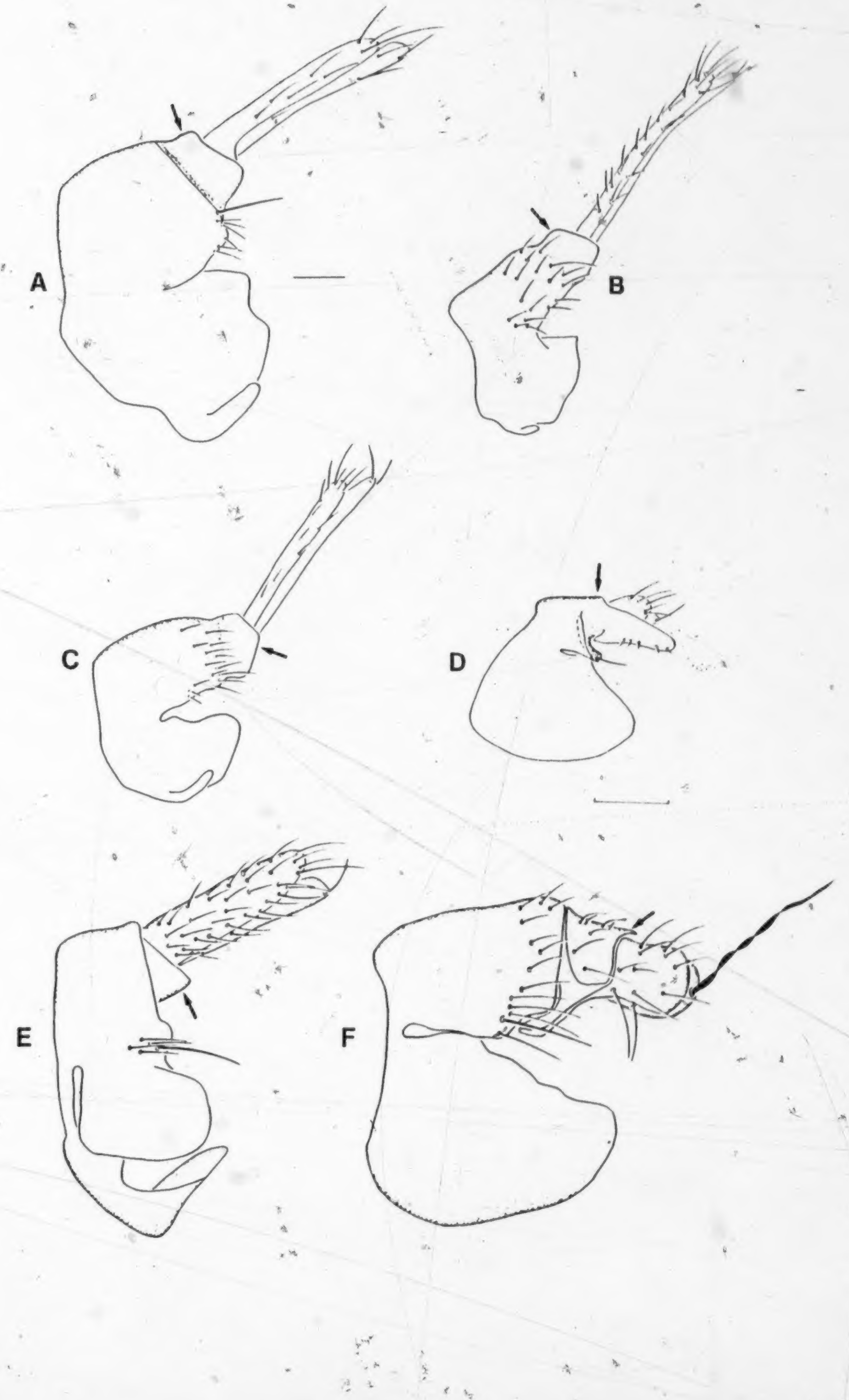

A
B
C
D
E
F

Fig. 6.3. A-F. Male terminalia, left lateral. A, *Diplonevra* species 12; B, *Diplonevra* species 10; C, *Diplonevra* species 7; D, *Diplonevra predicta* Disney; E, *Diplonevra nitidula* (Meigen); F, *Diplonevra gynaptera* Fuller & Lea. Scale bars = 0.1mm, all figures to same scale. Arrows indicate epandrial ring.

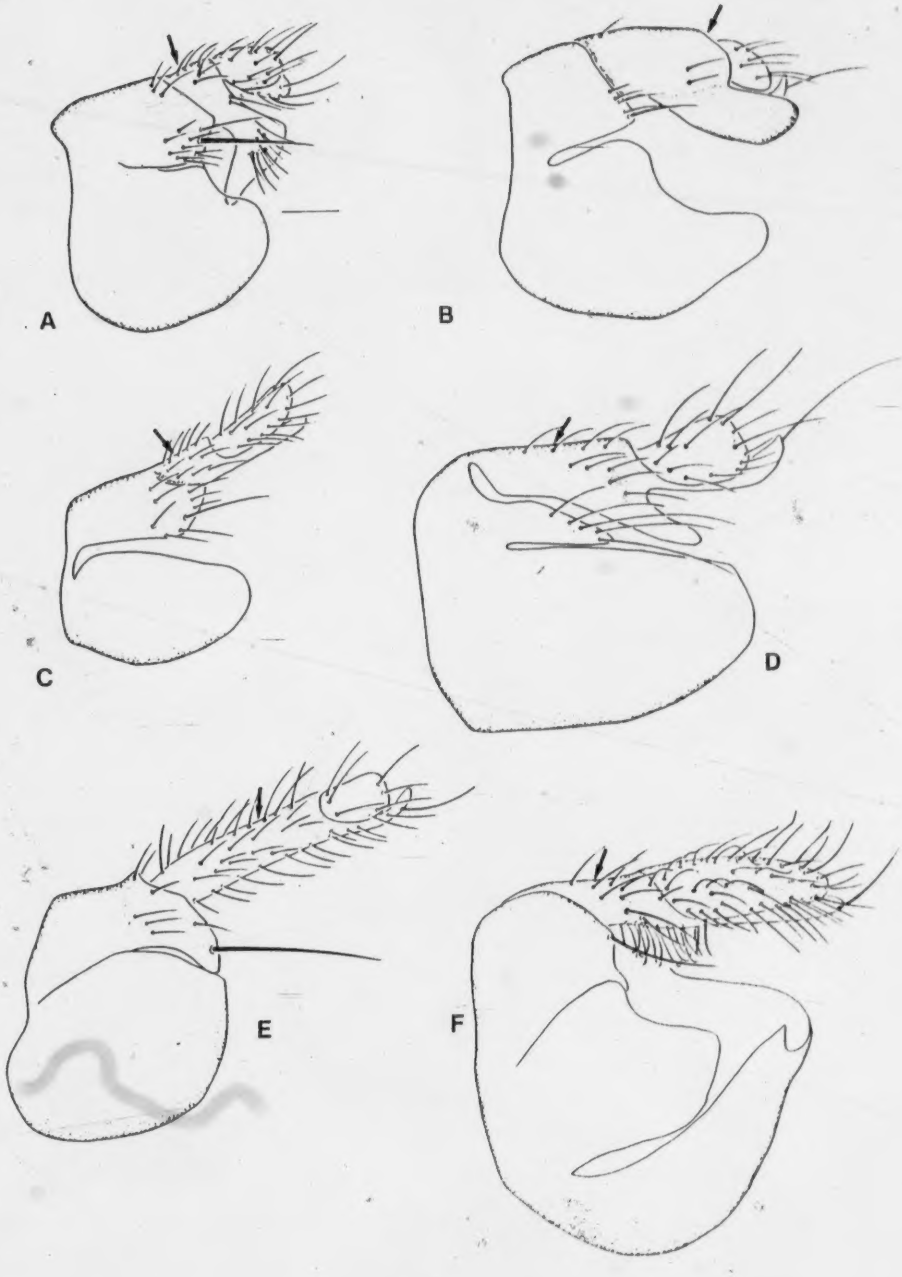

A
B
C
D
E
F

Fig. 6.4. Internal organs of female *Diplonevra* sp. Scale bar = 0.1mm. Abbreviations: ag - accessory gland, g - gut, o - ovary, r - rectum, rs - rectal stalk.

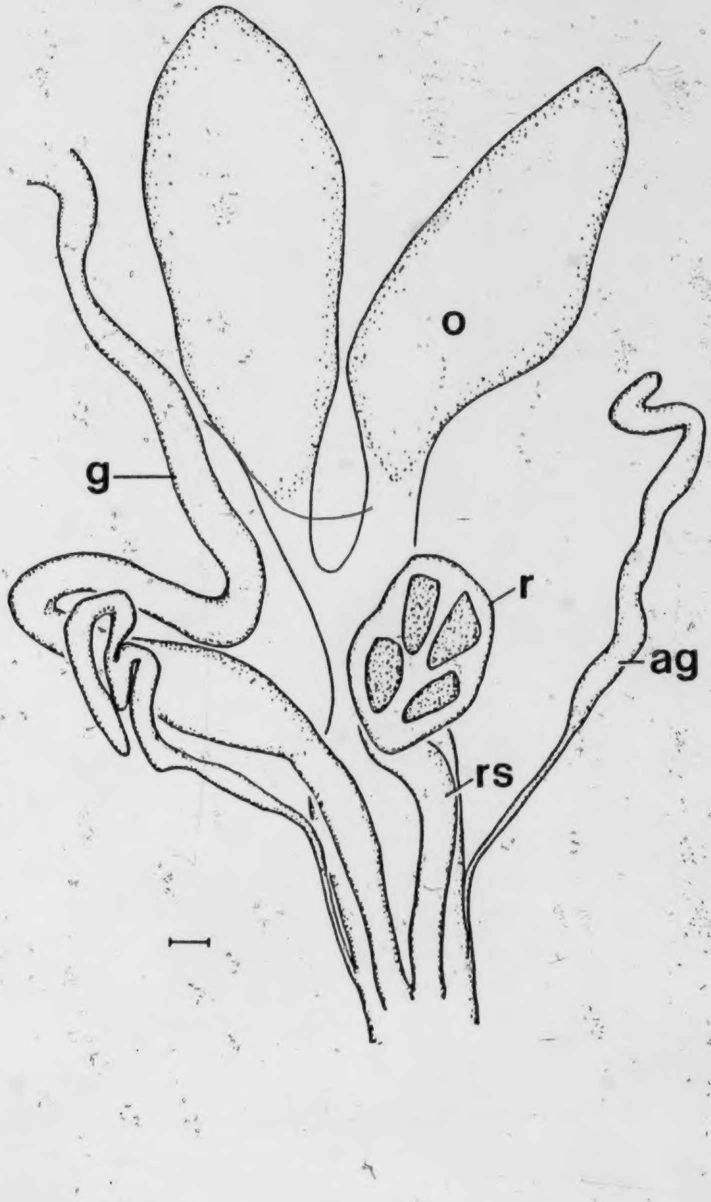
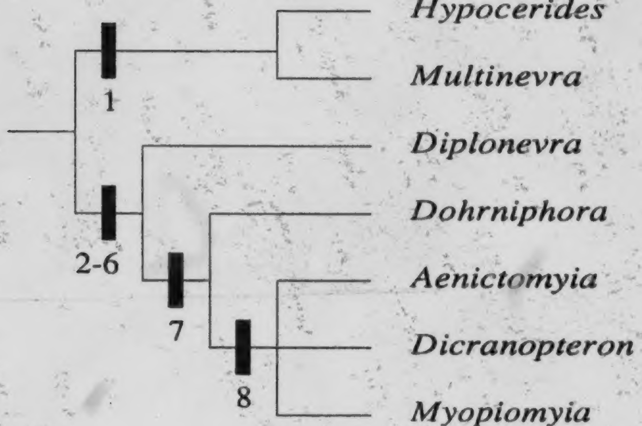

o
g
r
ag
rs

Fig. 6.5. Hypothesis of phylogenetic relationships of Diplonevrini.


Hypocerides
Multinevra
Diplonevra
Dohrniphora
Aenictomyia
Dicranopteron
Myopiomyia
1
2-6
7
8

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7. REVISION AND PHYLOGENETIC CLASSIFICATION OF GENERA OF SUBFAMILY CONICERINAE (DIPTERA: PHORIDAE)

> The taxonomic position of *Cyphometopis* and *Ceratusa* is not clear.. future studies of the male genitalia may help to solve this problem (Borgmeier, 1967).

7.1 Introduction

This subfamily contains one of the most infamous phorid flies, the coffin fly, *Conicera tibialis* Schmitz, an organism often found in vast numbers in buried corpses. Other conicerines are much less well-known, and their relationships have not been hypothesized previously. Formerly all of these taxa were classified in the paraphyletic subfamily Phorinae, a grouping that has been shown recently to be unnatural (Chapter 3). Below, the relationships of the constituent taxa of this subfamily are hypothesized, and their male terminalia illustrated.

7.2 Materials and Methods

The specimens examined in this study were from my own collection (abbreviated as BVB) and from the Canadian National Collection (CNC), Biosystematics Research

Centre, Agriculture Canada, C.E.F., Ottawa, Ontario, Canada, K1A 0C6 (curator J.M. Cumming).

Male terminalia were examined by treatment in hot 10% KOH, and rinses of 30% acetic acid, water, and alcohol. They were then placed in an evaporating dish with a drop of glycerine and about 2ml of alcohol, and were put on a warming tray to allow the alcohol to evaporate. Terminalia were then placed in glycerine jelly on glass slides and examined with light microscopy.

Some specimens were gold-coated and examined with a Cambridge 100 Scanning Electron Microscope.

Hypothesized relationships were reconstructed using standard cladistic techniques (Hennig, 1966). The cladogram was constructed manually.

7.3 Terms

Recent reviews of Diptera phylogeny have postulated adelphotaxon (Griffiths, 1972), ancestor-descendant (Chvála, 1983) or no special relationship (McAlpine, 1989) between the Orthogenya and Cyclorrhapha. This disagreement affects the terms used to refer to the male genitalia, and I deal with it as I have previously (Brown, 1987).

The terms synapotypic, apotypic, plesiotypic etc. have been used in this paper as more general terms, rather than synapomorphic, apomorphic, plesiomorphic and so on which refer only to structure (Chapter 2, Terms). Other terms not used by Hennig, but subsequently proposed by Ax (1987) are used in this work: adelphotaxon (=sister-group) and groundpattern (=groundplan). The reasons for preferring the use of these more recent terms are those of Ax (1987).

7.4 Reconstructed phylogeny of Conicerinae

Discussion of hypothesized synapotypic character states.

The monophyly of this group was established previously (Chapter 3), based on surstyli fused to epandrium, flagellomere 1 elongate in male and frons short. The cladogram (Fig. 7.3) was constructed using the following character states:

1 Wing vein R_{2+3} absent.

2 Hypandrium with round lobe (Figs. 7.2C-F, hl).

3 Epandrium with short, peg-shaped setae (Figs. 7.1B, p).

7.5 Classification

This classification depicts the relationships of the taxa using sequencing and subordination. Taxa equally indented are adelphotaxa; when there are more than one such group they are successive adelphotaxa, unless labelled ***sedis mutabilis*** (Wiley, 1981).

SUBFAMILY CONICERINAE

Ceratusa Borgmeier ***sedis mutabilis***

Cyphometopis Borgmeier ***sedis mutabilis***

Gymnoptera Lioy

Contopteryx Schmitz

Darwiniphora Schmitz

Conicera Meigen

7.6 Revision of genera

SUBFAMILY CONICERINAE LIOY 1864

Type genus: *Conicera* Meigen 1830

Diagnosis. Frons of male short; male flagellomere 1 elongate, conical.

Geographic distribution. Found worldwide.

Phylogenetic relationships. This subfamily is part of a tritomy including the

Aenigmatiinae and Metopininae (Chapter 3).

Known fossil material. One species, *Conicera eocenica* Meunier, was described from Baltic amber. A further specimen, of either *Conicera* or *Gymnoptera*, is in the Dominican (Oligocene age) amber collection of B.V.Brown and D.H.Feener (BVB).

Included taxa. Ceratusa Borgmeier (Central America), *Cyphometopis* Borgmeier (Brazil), *Gymnoptera* Lioy (worldwide), *Contopteryx* Schmitz (south Chile, south Argentina), *Darwiniphora* Schmitz (south Chile), *Conicera* Meigen (widespread), and an undescribed genus from New Zealand.

7.6.1 *Ceratusa* Borgmeier 1967

(Fig. 7.2A)

Type species: *Ceratusa crinicornis* Borgmeier 1967 (by original designation).

Derivation of generic name. This name is derived from a Greek word for horn, referring to the enlarged male flagellomere 1.

Diagnosis. Antennal cavities extended to one-half length of frons in male. Wing vein

R_{2+3} present.

Way of life and immature stages. Unknown.

Collecting methods. I have not collected specimens of this genus, but Malaise traps apparently capture adults.

Geographical distribution. Neotropical Region: Costa Rica, Guatemala.

Phylogenetic relationships. This genus, and *Cyphometopis* are the relatively primitive adelphotaxa of the rest of the conicerines.

The monophyly of this genus, relative to *Cyphometopis* (below) is doubtful. The wing venation is extremely similar, and Borgmeier's (1924) description of the male terminalia of *Cyphometopis carinifrons* is similar to the structure I observed in male *Ceratusa crinicornis* (Fig. 7.2A). The main difference between the two genera is the extent of the antennal cavities on the frons, but the state found in males of *Ceratusa*, extending only halfway up the frons, is clearly just a primitive state relative to the even larger cavities in males of *Cyphometopis*.

Hypothesized autapotypic character states of *Ceratusa* cannot be proposed at this time, until the relationships between this genus and *Cyphometopis* are clarified.

Number of recognized species. One.

*Material examined. **C. crinicornis*** **Borgmeier**, COSTA RICA: 1♀, Puntarenas: road to Rincon, 24km W Pan-American Highway, 200m, iii.-iv.1988, Malaise trap, P.Hanson & I. Gauld (BVB), GUATEMALA: 2♂, Zacapa, San Lorenzo, 2300m, 13-17.xi.1986, M. Sharkey, Malaise trap, cloud forest (BVB).

7.6.2 *Cyphometopis* Borgmeier 1924

Type species: *Cyphometopis carinifrons* Borgmeier 1924 (by original designation).

Derivation of generic name. This name is derived from Greek, meaning "humped-forehead", apparently referring to the raised, narrow frons.

Diagnosis. Antennal cavities extended to vertex, such that frons is reduced to thin medial strip (Borgmeier, 1924, Fig. 1). Wing vein R_{2+3} present.

Way of life, immature stages and collecting methods. Unknown.

Geographical distribution. Neotropical Region: Brazil.

Phylogenetic relationships. See *Ceratusa*.

Hypothesized autapotypic character states of *Cyphometopis* include the following:

1 Antennal cavities of male extended to vertex.

Number of recognized species. Three.

Material examined. None.

7.6.3 *Gymnoptera* Lioy 1864

(Fig. 7.2B)

Type species: *Phora vitripennis* Meigen (by monotypy).

Derivation of generic name. This name is derived from Greek and refers to the non-setose wing (Lioy, 1864); it seems to be a misnomer, however, as the costa in specimens I have examined has definite setae.

Diagnosis. Wing vein R_{2+3} absent. Huge setae present on posteroventral margin of left side of male epandrium (Fig. 7.2C).

Way of life and immature stages. Larvae of species of this genus are scavengers. Adults of *G. molluscovora* (Bohart) feed and oviposit on rotting molluscs, which is a suitable medium for larval development (Bohart & Gressitt, 1951, as ***Parafannia***). Adults of *G. simplex* (Brues) are attracted to carrion, those of *G. orientalis* (de

Meijere) have been reared from a rotting beetle (Coleoptera) larva (Schmitz, 1953), and *G. neotropica* Borgmeier have been reared from a dead carabid beetle (Borgmeier, 1969a). Disney (1983) examined much conflicting anecdotal evidence and determined that *G. vitripennis* is associated with *Vespula* (Hymenoptera: Vespidae) nests, whereas *G. longicostalis* Schmitz breeds in *Bombus* (Hymenoptera: Apidae) nests; there is no information on their way of life in these nests. Both of these species, however, also were reared from a single caterpillar of *Cossus cossus* (Lepidoptera: Cossidae) (Disney, 1983). Adults of at least *G. longicostalis*, and possibly also *G. vitripennis*, visit flowers (Baumann, 1978a, b; Disney, 1980a).

The immature stages were described by Schmitz (1953).

Collecting methods. I have not collected specimens of this genus, but carrion-baited traps should attract adults.

Geographical distribution. Palearctic, Neotropical, Oriental and Australasian Regions.

Phylogenetic relationships. This genus is the adelphotaxon of *Contopteryx* + *Darwiniphora* + *Conicera*.

Hypothesized autapotypic character states of *Gymnoptera* include the following:

1 Male with huge setae present on left side of epandrium.

2 Larva with long, lateral body processes (Schmitz, 1953, Fig. 169a, Schmitz, 1955 Fig. 202).

Number of recognized species. Six.

Material examined. G. longicostalis **Schmitz**, 1♂, ENGLAND: Devon, Torquay, 25.vi.1960, J.R.Vockeroth (CNC); ***G. neotropica* Borgmeier**, 1♂, WEST INDIES: St. Kitts, Wingfield Mt., 400m, 1-30.xi.1985, L.D.Coote, Malaise trap, old field/forest (BVB); *G. vitripennis* **(Meigen)**, 1♂, ENGLAND: Devon, Paignton, 6.ix.1960, J.R.Vockeroth (CNC).

7.6.4 *Contopteryx* Schmitz 1929

(Fig. 7.2C)

Type species: *Contopteryx illustris* Schmitz 1929 (by original designation).

Derivation of generic name. This name is derived from Greek words meaning short wing, referring to the reduced wing found in adult female specimens.

Diagnosis. Wing vein R_{2+3} absent. Male epandrium with long, ventrally directed lobe on left side; hypandrium with rounded lobe (Fig. 7.2C). Female brachypterous, wing rudiment long, rod-shaped (illustrated by Schmitz, 1929, Fig. 5).

Way of life and immature stages. Unknown.

Collecting methods. These flies have been collected in Malaise, pan and flight-intercept traps.

Geographical distribution. Neotropical Region: southern Chile and Argentina.

Phylogenetic relationships. This genus is the adelphotaxon of *Darwiniphora* + *Conicera.*

Autapotypic character states of *Contopteryx* include the following:

1 Male with 8-10 large setae on hind tibia.

2 Female with numerous autapotypies, such as eyes reduced, scutellum absent, wings reduced to narrow rods, halter absent.

Number of recognized species. One.

Material examined. ***C. illustris*** **Schmitz**, CHILE: 1♀, Chiloe Island, 70m, Ahori Alto, primary forest, 22.ii.1988, L.Masner (BVB), 1♂, iv.1988, Malaise trap, L.E.Peña (BVB), Osorno, 2♂, 2♀, Puyehue N.P., Antillanca, 1300m, 15-16.ii.1988, pan trap, *Nothophagus* tree line, L. Masner (BVB), Valdivia, 2♂, 500m, 30km W La Union, Las Trancas, *Nothophagus*, 7-11.ii.1988, pan trap, L.Masner (BVB).

7.6.5 *Darwiniphora* Schmitz 1953

(Fig. 7.2D)

Type species: *Conicera dupliciseta* Schmitz 1929 (by original designation).

Derivation of generic name. This genus was named after Charles Darwin, who collected specimens of the type species on his famous voyage around South America.

Diagnosis. Supra-antennal setae absent. Lower interfrontal setae convergent, porrect. Wing vein R_{2+3} absent. Hind tibia with basal pair of setae, one dorsal, one anterodorsal.

Way of life and immature stages. Unknown.

Collecting methods. A wide range of collecting methods, such as pan, Malaise and flight-intercept traps, will procure adult specimens of this genus.

Geographical distribution. Neotropical Region: southern Chile.

Phylogenetic relationships. This genus is the adelphotaxon of *Conicera*.

The monophyly of this genus relative to *Conicera* is doubtful, but its relationships should be made apparent after the genus *Conicera* is revised by Dr. J.K. Barnes (work in progress).

Hypothesized autapotypic character states of *Darwiniphora* include the following:

1 Supra-antennal setae absent.

2 Lower interfrontal setae convergent, porrect.

Number of recognized species. Two.

Material examined. ***D. dupliciseta*** **Schmitz**, 2♂, CHILE: Osorno, Puyehue N.P., Antillanca, 1300m, 15-16.ii.1988, pan trap, *Nothophagus* tree line, L. Masner (BVB).

7.6.6 *Conicera* Meigen 1830

(Figs. 7.2E-F)

Type species: *Conicera atra* Meigen 1830 = *Conicera dauci* (Meigen) 1830

Derivation of generic name. This name is derived from Latin words meaning cone-shaped antenna.

Diagnosis. Supra-antennal setae present. Lower interfrontal setae close together, divergent, reclinate. Wing vein R_{2+3} absent. Hind tibia with basal pair of setae, one dorsal, one anterodorsal.

Way of life and immature stages. Adults of most species of the genus are reared from decaying organic material; examples include the well known, carrion-feeding "coffin fly", *Conicera tibialis* (Borgmeier, 1969b; Colyer, 1954a, b, c), species reared from decaying vegetable matter (Colyer, 1954d, 1957) and fungi (Disney & Evans, 1988; Smith, 1956). Many are also known to visit flowers (Baumann, 1978a, b; Disney, 1980a), and others have been found in mammal burrows (Baumann, 1977; Hackman, 1963, 1967), caves (Leruth, 1936), and reared from soil (Disney, 1980b; Disney & Gunn, 1980; Disney *et al.*, 1981).

Immature stages are described by Schmitz (1953).

Collecting methods. I have collected these flies with Malaise, flight-intercept and pan traps. Baiting with suitable decaying material and collecting from flowers should also produce specimens.

Geographic distribution. Worldwide, except Africa and Australia.

Phylogenetic relationships. This genus is the adelphotaxon of *Darwiniphora* Schmitz (south Chile), which may itself be part of *Conicera*. Their terminalia (Figs. 7.2D-F) are extremely similar.

Autapotypic character states of this genus cannot be hypothesized at this time, as most possibilities also occur in *Darwiniphora*.

Number of recognized species. Twenty.

Material examined. Most of my specimens of *Conicera* were loaned to Dr. J.K. Barnes (Biological Survey, Rm 3132, Cultural Education Center, Albany, NY, 12230, USA) for his revisionary work on the genus. The following specimens were retained for this study: ***Conicera* sp.1**, 1♂, COSTA RICA: Puntarenas, Monteverde, 1700m, 1-5.vi.1988, Malaise trap, B.V.Brown, stunted forest (BVB); ***Conicera* sp.2**, 1♂, COSTA RICA: Heredia, Puerto Viejo de la Sarapiquí, La Selva Biological Station, 40m, 23-26.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50 (BVB); ***Conicera* sp.3**, 1♂, COSTA RICA: Heredia, Puerto Viejo de la Sarapiquí, La Selva Biological Station, 40m, 16-23.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50 (BVB); ***Conicera* sp.4**, 1♂, COSTA RICA: Puntarenas, Monteverde, 1700m, 28.v.-1.vi.1988, Malaise trap, B.V.Brown, stunted forest (BVB); ***Conicera* sp.5**, 1♂, ECUADOR: Pichincha, 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown & L.Coote, Malaise trap, rain forest, 189m (BVB); ***Conicera* sp.6**, 1♂, VENEZUELA: Lara, Yacambú, 1200m, 7.v.1981, H.Townes, Malaise trap (BVB); ***Conicera* sp.7**, 1♂, ECUADOR: Pichincha, 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown & L.Coote, Malaise trap, rain forest, 189m (BVB); ***Conicera* sp.8**, 1♂, ECUADOR: Pichincha, 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown & L.Coote, Malaise trap, rain forest, 189m (BVB); ***Conicera* sp.9**, 1♂, THAILAND: 70km SW Chiang Mai, Doi Inthanon National Park, 7.ii.1989, T.W.Thormin, 1570m, wet, evergreen forest, pan trap (BVB)

7.7 Conclusions and suggested future work

More research is needed to substantiate the relationship between the basal two genera *Cyphometopis* and *Ceratusa*, and the rest of the conicerines, as the character state used to group them occurs several times within the Phoridae. Similarly, the loss of wing vein R_{2+3} is a relatively tenuous character state with which *Gymnoptera* is grouped with *Contopteryx*, *Darwiniphora* and *Conicera*. The character states grouping these last three genera are much more convincing, and indicate a well-supported group. Further research will probably show that the genus *Ceratusa* is a synonym of *Cyphometopis*, and that *Darwiniphora* is a synonym of *Conicera*. These synonymies would leave the relationships between the four remaining genera unchanged. Hopefully, the revision of *Conicera* by Dr. Barnes will solve some of the taxonomic problems, and discovery of further new conicerines, such as an undescribed genus in my collection from New Zealand, will allow further resolution of the generic classification of these flies.

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Table 7.1. Distribution of plesiotypic and synapotypic character states among the genera of Conicerinae. 0 - plesiotypic, 1 - synapotypic.

Characters	123
Taxa	
Ceratusa	000
Cyphometopis	000
Gymnoptera	100
Contopteryx	110
Darwiniphora	111
Conicera	111

Fig. 7.1. A-B. *Conicera* sp. A, Male terminalia, posterior; B, surstyli of male terminalia. Abbreviations: p - peg-like setae.

A
B
p
p

Fig. 7.2. A-F. Male terminalia, left lateral. A, *Ceratusa crinicornis* Borgmeier; B, *Gymnoptera neotropica* Borgmeier; C, *Contopteryx illustris* Schmitz; D, *Darwiniphora dupliciseta* Schmitz; E, *Conicera barberi* (Malloch); F, *Conicera* sp.1. Scale bar = 0.1mm, all figures to same scale. Abbreviation: hl - hypandrial lobe.

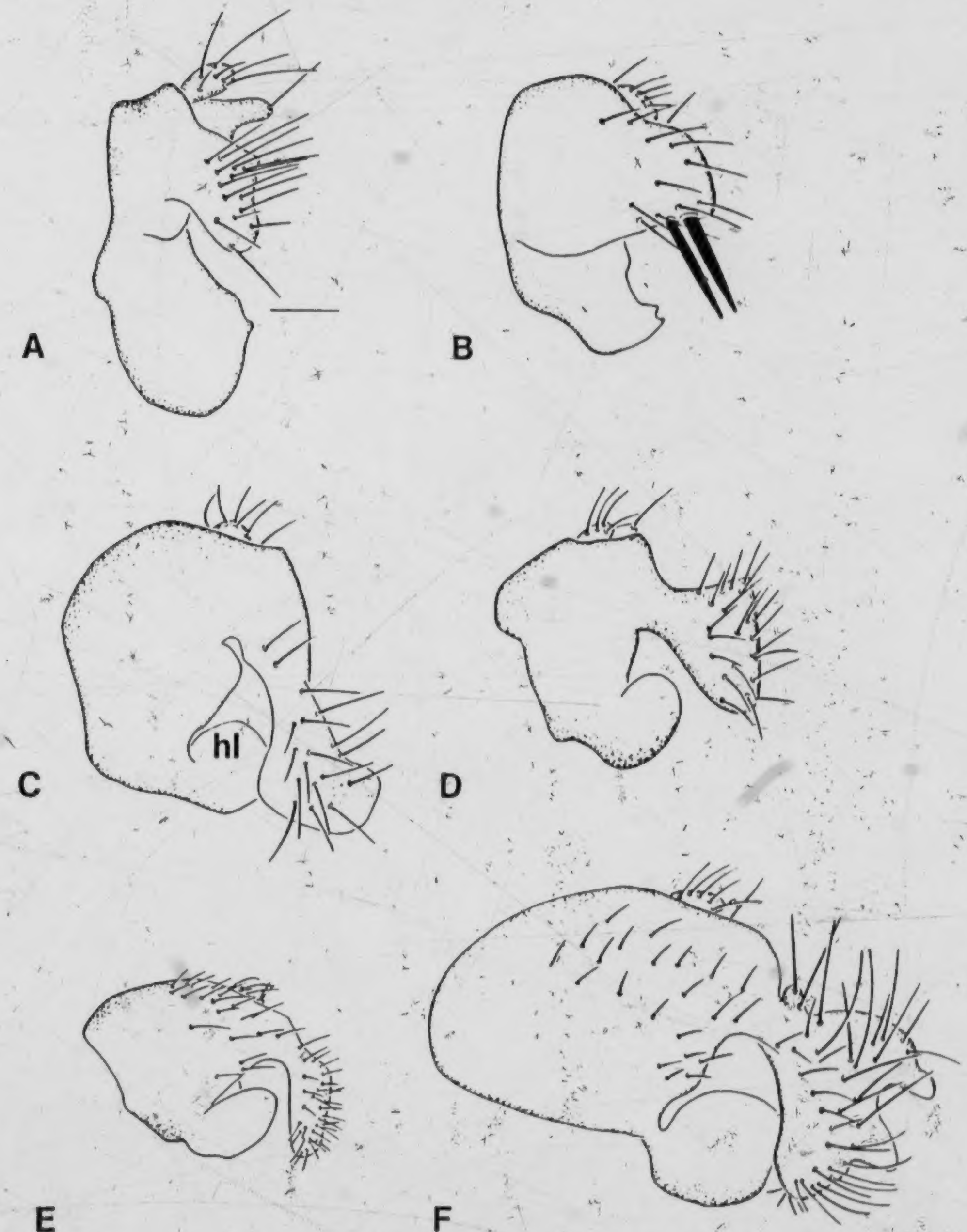
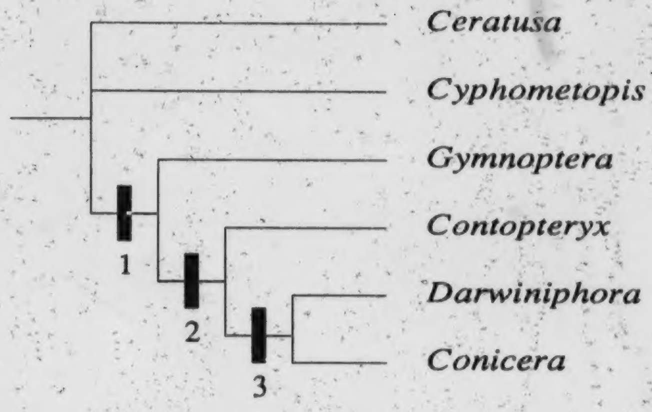

A
B
hl
C
D
E
F

Fig. 7.3. Hypothesized phylogenetic relationships of Conicerinae.


Ceratusa
Cyphometopis
Gymnoptera
Contopteryx
Darwiniphora
Conicera
1
2
3

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8. SUBFAMILY METOPININAE: DIAGNOSES AND PHYLOGENETIC CLASSIFICATION OF GENUS-GROUPS, AND REVISION OF GENERA OF THE NEARCTIC REGION (DIPTERA: PHORIDAE)

8.1 Introduction

The subfamily Metopininae contains the majority of described phorid genera and species, including the vast, paraphyletic genus *Megaselia* Rondani. In his revision of the family Phoridae, Schmitz (1929) divided the subfamily Metopininae into two tribes, the Metopinini Rondani (1856, emended by Schmitz, 1926a) and Beckerinini Enderlein (1936, emended by Schmitz, 1926a). The monophyly of neither of these taxa has been demonstrated adequately. More recently, Disney (1989a) proposed the first higher level cladistic relationships within the subfamily, identifying a monophyletic group he named tribe Megaseliini.

This paper investigates further the higher level classification of the Nearctic Metopininae.

8.2 Materials and methods

Material examined in this study was from my own collection (abbreviated as BVB) and from the collection of the Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), Adena[illegible]rallee 150-164, D-5300, Bonn 1, Federal Republic of Germany (curator H. Ulrich).

Taxa from outside of the Nearctic Region frequently were used for comparison and to test hypotheses based on Nearctic specimens. Because of our limited knowledge about the Neotropical, Oriental, Australasian and Afrotropical phorid faunas, many of the species from these regions were not identified to species. This is in recognition of the incomplete coverage given by existing keys, as well as the realization that there are a great many undescribed species in regions outside of North America and Europe.

Full taxonomic synonymies are not given in this paper, except for those not found in Borgmeier (1968, 1971).

Male terminalia were examined by treatment in hot 10% KOH, and rinses of 30% acetic acid, water, and alcohol. They were then placed in an evaporating dish with a drop of glycerine and about 2ml of alcohol, and were put on a warming tray to allow the alcohol to evaporate off. Terminalia were then placed in glycerine jelly on glass slides and examined with light microscopy.

Some specimens were gold-coated and examined with a Cambridge 100 Scanning Electron Microscope.

Hypothesized relationships were reconstructed using standard cladistic techniques (Hennig, 1966). The cladogram in this paper was constructed manually, without computer algorithms. The data set was subsequently checked with the computer program Hennig-86 (Farris, 1989) to see if there were further equally parsimonious cladograms.

8.3 Terms

Recent reviews of Diptera phylogeny have postulated adelphotaxon (Griffiths, 1972), ancestor-descendant (Chvála, 1983) or no special relationship (McAlpine, 1989) between the Orthogenya and Cyclorrhapha. This disagreement affects the terms used to refer to the male genitalia, and I deal with it as I have previously (Brown, 1987b).

The terms synapotypic, apotypic, plesiotypic etc. have been used in this paper as more general terms, rather than synapomorphic, apomorphic, plesiomorphic and so on that refer only to structure (Chapter 2, Terms). Other terms not used by Hennig, but subsequently proposed by Ax (1987) are used in this work: adelphotaxon (=sister-group) and groundpattern (=groundplan). The reasons for preferring the use of these more recent terms are those of Ax (1987).

8.4 Reconstructed phylogeny of the Metopininae

It was not possible to resolve completely the phylogeny of this group. The large number of component taxa, most of which occur outside of the Nearctic Region, and the many species of *Megaselia* make reconstructing the phylogeny of this group a gigantic task. The relationships of the basal lineages, however, inferred in part previously (Chapter 3) are treated in greater detail. Further resolution of the phylogeny of the *Megaselia*-group of genera is also possible.

Tribal Classification of Metopininae.

The three currently recognized tribes of the Metopininae are Beckerinini, Metopinini and Megaseliini. The Beckerinini contains metopinine taxa that have not diverged substantially from the basal lineage groups, and is paraphyletic (Chapter 3). The tribe was recognized by the possession of an anepisternal furrow and forward-pointed (porrect) or upwards-pointed (reclinate) supra-antennal setae. Porrect and reclinate supra-antennal setae, however, are found also in primitive-grade phorids, and their presence is obviously a primitive character state that cannot be used to define a monophyletic taxon. Schmitz (1939a) proposed that the character inner scutellar setae smaller than outer setae might be a defining character of beckerinines. Because smaller inner scutellar setae are present in species of the genus *Rhopica* that apparently belong in a more basal position than the other Beckerinini, it seems that this character state cannot be used to characterize this group either (see below).

The Metopinini includes all non-beckerinine Metopininae, or all metopinines with downwards-pointed (proclinate) supra-antennal setae. This character state is likely a valid one, but Disney (1989a) pointed out some problems, namely that some genera lack supra-antennal setae and that the supra-antennal setae of some genera are of dubious homology. These exceptions are probably secondarily derived, however, and may not justify rejection of this character state.

Disney (1989a) proposed a well founded monophyletic group, the tribe Megaseliini, that subsumes part of the Metopinini. Unfortunately, the ranking of this group as a tribe is too high. The basal dichotomy in the Metopininae is in fact between *Triphleba* and rest of the Metopininae (as shown below); therefore, the Megaseliini must be reduced in rank. I propose that this group be called simply the *Megaselia*-group, an informal taxonomic name, until the basal relationships of the subfamily are resolved fully. Another difficulty with the concept of the Megaseliini is that many of the taxa that must be included in this monophylum lack the major synapotypy of this group: a Dufour's mechanism in the female crop. As shown below, it is more parsimonious to include many parasitic genera in the Megaseliini despite their lack of a Dufour's mechanism. Thus the small, well circumscribed group identified by Disney has become swamped with many of the other metopinine genera.

The final group of metopinines is the *Metopina*-group of genera. These flies form a cohesive group as the adelphotaxon of the *Megaselia*-group of genera.

Hypothesized synapotypic character states (see also Table 8.1)

1 Basal hypandrial setae present. (Fig. 3.1E in Chapter 3; Figs. 50-51 in Brown, 1987b)

2 Anepisternal furrow distinctly present. (Fig. 3.1D in Chapter 3)

3 Inner scutellar setae larger than outer.

4 Male terminalia divided (Fig. 3.4C in Chapter 3)

5 U-shaped tergite present in female abdomen.

6 Tergite 7 present in female abdomen (reversal to state found in phorid outgroups).

7 Tergite 8 present in female abdomen (reversal to state found in some phorid outgroups).

8 Supra-antennal setae proclinate (pointed ventrally) (Fig. 3.1B in Chapter 3).

9 Dufour's mechanism present in female crop.

10 Male terminalia markedly asymmetrical, with hypandrium anteriorly displaced and normal ventral portion deflected to right lateral side.

11 Wing vein R_{2+3} absent.

8.5 Classification

This classification depicts the relationships of the taxa using sequencing and subordination. Taxa equally indented are adelphotaxa; when there are more than one such group they are successive adelphotaxa, unless labelled *sedis mutabilis* (Wiley, 1981).

SUBFAMILY METOPININAE

Triphleba Rondani

MONOPHYLUM 2 (unnamed)

Rhopica Schmitz (not Nearctic)

MONOPHYLUM 3 (unnamed)

Beckerina Malloch

MONOPHYLUM 4 (unnamed)

Megaselia-group

Metopina-group

Notes on primitive grade Metopininae. The genera *Triphleba, Beckerina* and other taxa previously classified as Beckerinini are inadequately characterized. The genus *Beckerina* was said to differ from *Megaselia* (Borgmeier, 1963) by the presence of porrect supra-antennal setae and hind tibia without dorsal longitudinal rows of setae. Both of these character states are primitive with respect to the primitive grade phorids (Hypocerine, Aenigmatiinae, Phorinae and Conicerinae), and there are exceptions to the second of these character states: some *Beckerina* have one or more dorsal setal rows. The following taxa have been described in the Beckerinini: *Aphiura* Schmitz (New Zealand; male only), *Anaclinusa* Borgmeier (Brazil; female only), *Beckerina* Malloch (worldwide except Afrotropical Region), *Brachyphlebina* Borgmeier and Prado (Brazil), *Chaetaspidia* Borgmeier (Costa Rica; male only), *Corynusa* Schmitz (South Chile); *Distichophora* Schmitz (Australia, New Zealand; male only), *Exochaeta* Schmitz (South Argentina; male only, but undescribed female examined); *Lecanocerus* Borgmeier (Nearctic and Neotropical Regions); *Macroselia* Schmitz (South Chile, Burma, New Zealand); *Paraphiura* Beyer (Tasmania; male only); and *Rhopica* Schmitz (New Guinea, Borneo). Of these, Peterson (1987) removed *Lecanocerus* to the

Metopinini, *Rhopica* and *Aphiura* (Fig. 8.3B) belong near *Triphleba* in the primitive grade Metopininae, and three genera, *Anaclinusa*, *Exochaeta* and *Brachyphlebina*, have sclerotized ovipositors, and thus probably belong to the *Apocephalus*-group of genera. Adults males of *Corynusa* have divided male terminalia (Fig. 8.3C), as do those of *Exochaeta* (Fig. 8.3D) and *Macroselia* (8.3E).

Similarly, the genus *Triphleba* was diagnosed by reduced anterior setae at apex of mid-tibia, a character state useful relative to some primitive grade phorids that keyed out near *Triphleba* (notably *Spiniphora*), but not useful relative to other Phoridae.

8.6 Revision of genera

SUBFAMILY METOPININAE Rondani 1856

Type genus: *Metopina* Macquart 1835 (by monotypy).

Diagnosis. Anepisternum with at least faint furrow in species of most genera. Hypandrium with posteroventral pair of setae.

Geographical distribution. Worldwide.

Phylogenetic relationships. This subfamily is possibly the adelphotaxon of the subfamily Conicerinae or of Aenigmatiinae.

8.6.1 *Triphleba* Rondani 1856

Citrago Schmitz, Disney 1982

Type species: *Triphleba hyemalis* Rondani Rondani, 1856 (original designation) = *T. hyalinata* (Meigen).

Derivation of generic name. This name, translated from Greek, means three-veined, and probably refers to the three radial wing veins.

Notes on synonymy. Disney synonymized *Triphleba* with *Citrago* because the diagnostic characters used to separate them in keys formed a gradient with no discernible gaps. Species of undoubted *Citrago* that I have examined, however, show a distinct aedeagal form with extremely long, thin processes, that may warrent recognition of the genus. Such separate generic recognition can be made only after a phylogenetic analysis shows that all *Triphleba* are more closely related to each other than any is to *Citrago*.

Diagnosis. Tibiae with large setae. Epandrium with one or both surstyli greatly elongate.

The characterization of this genus by autapotypic character states is difficult, as there are few characters that are not shared by some other closely related genera. The genus *Conicera* Meigen also has enlarged surstyli, although they are typically downturned, and not elongate like those of most *Triphleba*. Males of the subgenus *Cerocratia* of the genus *Gymnophora* also have elongate surstyli, but these are probably secondarily derived (Brown, 1987a). The females of most *Triphleba* species have distinctly modified sternite 7, but this character state cannot be polarized until it is described for more species.

Way of life and immature stages. Larvae have been bred from divergent media, such as carrion, dead earthworms and untreated sewage sludge (*T. nudipalpis*, Colyer in Disney, 1980), fungi (*T. minuta* (Fabricius) and *T. trinervis* (Becker), Colyer, 1952b, 1954b) and debris and dead brood in wasp nests (*T. lugubris* (Meigen), MacDonald & Matthews, 1983; MacDonald *et al.*, 1975; personal observation in *Dolichovespula arenaria*). Additionally, adult females of *T. laticosta* Borgmeier have been bred from nests of *Camponotus herculeanus* (L.) in Ontario (new record).

Adults of many species of *Triphleba* display marked seasonality. Colyer (1952b) found *T. minuta* occurred almost always in the fall, at the same time its host mushroom appeared. In Edmonton, Alberta, I found *T. aequalis* Schmitz occurred only in the fall, whereas *T. labida* Borgmeier and *T. pachyneura* (Loew) were present only in the spring, and *T. lugubris* and other species were present from mid- to late summer. Adults of an undescribed species of this genus from Arizona occurred only in mid-winter.

The larvae of *T. minuta* were described briefly by Colyer (Colyer, 1952b), and other descriptions were listed by Hennig (1952).

Collecting methods. I have collected these flies only in Malaise traps, especially in the early spring and late fall.

Geographic distribution. Species of this genus are found throughout the Holarctic Region, as well as in Burma and the Neotropical Region (as *Citrago* in Borgmeier, 1968). Species formerly classified as *Triphleba* from New Zealand are now placed in a separate genus in the Hypocerinae (Brown in press). As Gotô and Takeno (1983) pointed out, *T. nipponica* Schmitz (Japan) probably does not belong in this genus; similarly *T. ctenochaeta* Beyer, *T. segrex* Beyer, and *T. schmitzi* Beyer (all from Burma) belong in a monophylum with *T. nipponica*, not with other *Triphleba* species.

Phylogenetic relationships. This genus is the adelphotaxon of the rest of the Nearctic Region Metopininae. Its relationships with *Rhopica* are unknown, although the two genera share some similarities, especially in the structure of the female mouthparts.

The genus *Triphleba* was classified previously as a member of the Phorinae, a group now known to be paraphyletic. The presence of the faint anepisternal furrow in some species apparently was overlooked, while the presence of tibial setae made it clear to earlier workers (e.g. Schmitz, 1939a) that *Triphleba* could not be a metopinine. The presence of basal hypandrial setae was noted by Schmitz, but he was apparently unaware of their importance.

According to illustrations given by Gotô (1985), *Rhopica* also belongs near the base of the Metopininae, as they also have fused terminalia and lack female tergite 7.

The character states of the fused epandrium/ hypandrium and lack of female tergite 7, characteristic of primitive phorids, conflict with the anterior scutellar seta larger than the posterior seta, a character state that Schmitz (1939a) thought linked *Rhopica* with the rest of the Beckerinini in the higher Phoridae. I give higher weight to the genitalic character states, but I have not seen actual specimens of *Rhopica*. It is possible that the fusion of the epandrium with the hypandrium is secondary in this genus; if so, then a monophyletic tribe Beckerinini could be supported. Possibly the character state of unequal scutellar setae in Beckerinini is similar to the states of fused epandrium and hypandrium and lack of female tergite 7 relative to taxa formerly classified as Phorinae; the outgroup evidence clearly shows that the condition is derived, yet any groupings inferred from these character states are paraphyletic, and a later loss must be hypothesized (Fig. 8.6). These three character states all support previously recognized groups that are not supported by other proposed synapotypic states; the fused epandrium/ hypandrium and the lack of female tergite 7 is contradicted by the presence of an anepisternal furrow and basal hypandrial setae in *Triphleba*, whereas unequal scutellar setae are contradicted by the presence of a divided epandrium/ hypandrium in most Beckerinini.

As seen in Fig. 8.6, all three of the hypothesized character reversals occur at the base of the *Beckerina* + Metopinini lineage. This problematic area suggests that a major evolutionary event took place at this junction, or that there is a major fault with the phylogenetic hypothesis put forward here. Any attempt, however, to derive the *Beckerina* + Metopinini lineage separately from the basal group phorids, *Triphleba* and

Rhopica results in the creation of unacceptable paraphyletic groupings.

Number of recognized species. There are a total of 84 recognized species; 23 occur in the Neartic Region (note in Borgmeier, 1968 *T. lugubris* and *T. aequalis* were not listed as occurring in North America, although he had recorded their presence previously in Borgmeier, 1963).

Nearctic Region material examined. ***T. aequalis* (Schmitz)**, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 13 males, 1 female, 22.ix.1986, 1 male, 24.ix.1987, 2 males, 28.ix.-4.x.1987, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB), Ontario: 1 male, Guelph, South Arboretum, 12-27.x.1984, B.V.Brown, Malaise trap, forest edge (BVB); ***T. bispinosa* (Malloch)**, CANADA: Ontario: 2 males, Guelph, South Arboretum, 26.ix.-3.x.1984, B.V.Brown, Malaise trap, forest edge (BVB); ***T. darlingtoni* (Borgmeier)**, CANADA: Alberta: Edmonton, Wagner Bog, 13-22.viii.1985, A.T.Finnamore, leg., pan trap 2 (BVB); ***T. forficata* Borgmeier**, CANADA: British Columbia: Burnaby, Burnaby Mt., 26.iv.1979, D. Gillespie (BVB); ***T. labida* Borgmeier**, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 45 males, 6-13.v., 8 males, 1 female, 13-22.v., 1 male, 22-26.v., 1 female, 26-29.v.1986, 1 male, 3-10.v.1988, B.V.Brown, Malaise trap, 3 males, 7-10.v.1986, T.G.Spanton, FIT, spruce/ poplar/ alder (BVB); ***T. laticosta* Borgmeier**, CANADA: Alberta: 1 male, Edmonton, University of Alberta Ecological Reserve, 24.ix.1987, B.V.Brown, spruce/ poplar/ aspen (BVB), Ontario: 4 females, Kirkwood, 13.vi.1966, C.Saunders, ex. nest of *Camponotus herculeanus* (BVB); ***T. lugubris* (Meigen)**, CANADA: Alberta: 2 males, 15 km S. Beaver Mines, Castle R. Bridge Campground, 23-29.vii.1986, T.G.Spanton, FIT, spruce/ fir (BVB), Edmonton, University of Alberta Ecological Reserve, 2 males, 5-15.vii., 1 male, 14-22.vii., 7 males, 18-25.viii.1986, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB), 1 male, Opal, 53°59'N, 113°13'W, 20-22.vii.1986, B.V.Brown, Malaise trap, sand, jackpine (BVB), Ontario, Guelph, South Arboretum, 1 male, 15-26.ix.1984, 1 male, 11-27.ix.1985, B.V.Brown, Malaise trap, forest edge (BVB), 1 male, Stouffville, 8-15.ix.1984, B.V.Brown, Malaise trap; ***T. pachyneura* (Loew)**, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 1 male, 6-13.v., 4 males, 13-22.v.1986, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB); ***T. palposa* (Zetterstedt)**, CANADA: Alberta: 5 males, 15 km S. Beaver Mines, Castle R. Bridge Campground, 23-29.vii.1986, T.G.Spanton, FIT, spruce/ fir (BVB); ***T. politifrons* (Borgmeier)**, CANADA: Ontario: Mainfleet Bog, 8km S. Welland, 4 males, 22-28.ix.1987, 1 female, 29.ix.-5.x.1987, A.Sterling, pan trap (BVB); ***T. subfusca* (Malloch)**, CANADA: Ontario, Guelph, South Arboretum, 1 male, 3-12.x.1984, B.V.Brown, Malaise trap, forest edge (BVB), 1 male, Mainfleet Bog, 8km S. Welland, 6-13.x.1987, A.Sterling, pan trap (BVB); ***T. sulcata* Borgmeier**, CANADA: Ontario: Guelph, South Arboretum, 1 male, 1 female, 12-27.x., 1 male, 2 females, 27.x.-7.xi.1984, 1 male, 5-7.vi., 1 male, 13-22.vii., 1 male, 22.vii.-6.viii., 1 male, 10-14.viii.1985, B.V.Brown, Malaise trap, forest edge, Malaise trap, wet shrubby meadow (BVB); ***Triphleba* undescribed species 1**, UNITED STATES: Arizona: Cochise Co., 12.5 km S. Sierra

Vista, Ramsey Canyon, 1 male, 26.xi.-3.xii., 1 male, 4 females, 3-10.xii., 4 males, 8 females, 17-24.xii., 7 males, 14 females, 24-31.xii.1986, 1 male, 3 females, 31.xii.-7.i.1987, 2 females, 7-14.i.1987, B.V.Brown, Malaise trap, 1700m, oak/ pine/ juniper (BVB).

Material examined from other zoogeographic regions. ***T. ctenochaeta*** **Beyer, 1♂**, BURMA: Kambaiti, 4.vi.1934, *Malaise* (ZFMK). Also, several specimens of *Triphleba* species, that were formerly classified as *Citrago*, from Costa Rica, Ecuador, and Venezuela were examined.

Monophylum 2

Diagnosis. Scutellar setae unequal, with anterior seta larger than posterior.

8.6.2 *Rhopica* Schmitz 1927b (not Nearctic)

No specimens of this genus were examined, but adult structure has been well illustrated by Gotô (1985). Nothing is known about the way of life or immature stages of the two described species of this genus. Both species are found in New Guinea.

Monophylum 3

Diagnosis. Tergite 7 present. Epandrium and hypandrium separate. U-shaped sclerite present.

8.6.3 *Beckerina* Malloch 1910b

Type species: *Phora umbrimargo* Becker 1901 (by monotypy).

Derivation of generic name. This genus was named after the Dipterist T. Becker, who described the type species.

Diagnosis. Supra-antennal setae porrect or reclinate. Anepisternum divided. Hind tibia of some species without dorsal, longitudinal setal row; other species with one or more sinuous rows. Epandrium/ hypandrium divided.

Notes on diagnosis. The definition of this genus is far from satisfactory. The following species have one dorsal, longitudinal setal row: *B. neotropica* Brues (Neotropical Region), *B. irregularis* Borgmeier (Brazil), *B. costaricana* Borgmeier (Costa Rica), *B. aliena* Malloch (USA), *B. dactylata* Borgmeier (West Indies), *B. luteihalterata* Borgmeier (Brazil) and a great number of undescribed species from the Neotropical Region. Two dorsal, longitudinal setal rows are present in the hind tibia of the following species: *B. fuscohalterata* Enderlein (Brazil), *B. polysticha* Schmitz (New Zealand), *B. nudipleura* Borgmeier (Brazil), *B. dominicana* Borgmeier (West Indies) and an undescribed species from Canada.

B. orphnephiloides lacks a frontal suture, has a hypandrial bridge and basal hypandrial setae (about 6), lacks heavy surstylar setation, basiphallus has lateral projection; therefore probably not congeneric with other "*Beckerina*"; *B. aliena* has a wavy, longitudinal, dorsal setal comb.

Way of life and immature stages. Unknown.

Collecting methods. There are no special techniques known to collect these flies, but they are frequently captured by Malaise traps.

Geographical distribution. Worldwide, except Africa.

Phylogenetic relationships. Beckerina is the adelphotaxon of the *Metopina*-group + the *Megaselia*-group.

Autapotypic character states of *Beckerina* cannot be hypothesized at this time, as the genus has not been properly defined yet.

Material examined. ***B. aliena*** **Malloch**, UNITED STATES: California: Shasta Co., 1♂, 3♀, 64km N Redding, 600m, 3-30.vi.1986, flight-intercept-trap, B.Brown & T.Spanton, pine/ spruce/ cedar/ oak (BVB); ***B. luteola*** **Malloch**, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 1♂, 29.v.-5.vi.1986, 1♂, 18-25.viii.1986, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB), Opal, 53°59'N, 113°13'W, 1♂, 20-22.vii.1986, 1♀, 17.23.viii.1986, B.V.Brown, Malaise trap, sand, jackpine (BVB), Ontario: Foote's Bay, shore of Lake Joseph, 1♂, 1♀, 11-30.viii.1985, 1♂, 30.viii.-15.ix.1985, B.V.Brown, Malaise trap, 2nd growth deciduous forest (BVB), Guelph, South Arboretum, 1♂, 15-26.ix.1984, 1♂, 25.vi.-3.vii, 1♂, 13-22.vii, 1♂, 19-27.vii.1985, B.V.Brown, Malaise trap, deciduous forest (BVB); ***B. orphnephiloides* Malloch**, 1♂, UNITED STATES: Oregon: 75km E Eugene, Andrews Experimental Forest (BVB); ***B. umbrimargo* (Becker)**, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 3♂, 13-22.v, 4♂, 26-29.v, 3♂, 29.v.-5.vi, 1♂, 12-20.vi.1986, 1♂, 3-10.v, 2♂, 18-25.v.1988, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB), UNITED STATES: Arizona: Cochise Co., 1♂, 18.5km W Portal, Basin Trail head, 7-10.vi.1986, B.V.Brown, Malaise trap, 1950m, oak/ pine/ juniper (BVB), near Portal, SWRS, 3♀, 20.vii.-2.viii.1965, V.Roth, Malaise trap, 2♀, 18-23.viii.1984, B.V.Brown, pan trap, intercept trap (BVB). Also, I examined numerous, unidentified specimens from the following countries: Canada, Costa Rica, Ecuador, Guatemala, Peru, United States, Venezuela.

Species: *B. aliena* Malloch, *B. similata* Malloch, .

Monophylum 4

Diagnosis. Supra-antennal setae proclinate (pointed downward).

8.6.4 *Metopina*-group

Diagnosis. Wing vein R_{2+3} absent. Female of most genera with wings reduced or absent. Gland opening on female tergite 5 large. Male terminalia with hypandrium displaced anteriorly.

Schmitz (1914) agreed with earlier authors that pulvilli and empodia were absent from females of this group, but both structures are in fact present on specimens I have examined.

Way of life. Many of these flies are associated with the colonies of social insects, especially ants and termites.

Fossils. There are undescribed fossil specimens of *Puliciphora* and *Metopina* in the Dominican amber collection of Brown and Feener (BVB), of approximately late Oligocene or early Miocene age. Both male and female specimens are represented. Grimaldi (1989) also noted the presence of adult specimens of *Metopina* in Chiapan (late Oligocene) amber, Dominican (early Miocene) amber and New Jersey (late Cretaceous) amber. He described a new species from the New Jersey amber specimen.

Geographical distribution. Widespread.

Phylogenetic relationships. This group is the adelphotaxon of the *Megaselia*-group of genera.

The genera included below form an easily recognized monophyletic group that has been acknowledged implicitly for a long time (for instance, by Schmitz 1914). Basing a revision of this group on the relatively depauperate Nearctic Region fauna would be premature, and would certainly not represent worldwide relationships. There are only eleven genera of these flies in the Nearctic Region, compared with forty-eight genera in the Neotropical Region alone. Of the eleven Nearctic Region genera, six are found only in the southern United States and northern México, and represent northern elements of a much more diverse Neotropical, myrmecophilous fauna. Most species of these six genera are associated with army ants (Hymenoptera: Formicidae: Ecitoninae).

Included Nearctic Region Genera. ***Acontistoptera*** Brues, ***Cataclinusa*** Schmitz, ***Chonocephalus*** Wandolleck, ***Commoptera*** Brues, ***Ecitomyia*** Brues, ***Ecitoptera*** Borgmeier and Schmitz, ***Metopina*** Macquart, ***Puliciphora*** Dahl, ***Stenophorina*** Borgmeier, ***Trophodeinus*** Borgmeier, ***Xanionotum*** Brues.

***Megaselia*-group**

Diagnosis. Dufour's crop mechanism present in female; if absent, sternite 8 elongate; females of many genera with parasitic-type ovipositor: segment 7 modified for positioning ovipositor or prying open sclerite, sternite 8 modified piercing stylet.

Way of life. Various species are predatory, parasitic, or scavengers (Ferrar, 1987)

Fossils. Fossil species of the *Megaselia*-group are known from Baltic amber (Brues, 1915, 1939), Dominican amber (Disney, 1987), Zanzibar copal (Brues, 1915), and Eocene Fushun amber (Hong, 1981).

Geographical distribution. Worldwide.

8.7 Reconstructed phylogeny of the *Megaselia*-group

Remarks. This group is the adelphotaxon of the *Metopina*-group of genera.

Disney (1989a) presented a hypothesis of the relationships of some taxa within his Megaseliini, but there were several problems associated with this cladogram (reproduced in Fig. 8.7A). The most important error was the arbitrary resolution of the clade including *Gymnophora* and "some *Megaselia*"; no synapotypy was given to justify this grouping. Furthermore, many taxa that Disney assigned to the Megaseliini were missing from this cladogram, so that the only terminal taxa depicted were *Megaselia*, *Gymnophora* and *Woodiphora*. Finally, some obviously non-monophyletic groups were depicted as being parts of a single lineage, such as the "rest" of the Metopininae. This cladogram can be redrawn to depict more accurately the information present in Disney's paper (Fig. 8.7B). The branches leading to the "rest of Phoridae" and the "rest of Metopininae" are deleted, as no new information is given on these probably non-monophyletic lineages.

Although originally proposed to contain only genera having a Dufour's mechanism, this exclusive definition of Megaseliini (= *Megaselia*-group) cannot be maintained. Adult females of *Apocephalus* have a distinct Dufour's mechanism present, but other genera that lack this structure have several other synapotypies with *Apocephalus*. Therefore, it is more parsimonious to postulate a loss of the Dufour's mechanism in these taxa than to exclude them and postulate separate derivations of the other character states.

A partial revision of the genera of this group is possible at this time.

Hypothesized synapotypic character states (see also Table 8.2)

1 Dufour's mechanism present (Figs. 8.2A-N).

2 Notopleural cleft present in adult male thorax (Fig. 8.1A).

3 Paired sternite 8 elongate in female ovipositor (Fig. 8.5A).

4 Female ovipositor deeply cleft (Figs. 8.5A-C).

5 Segment 7 in female markedly modified as prying mechanism for egg deposition (Figs. 8.1B-D).

The outgroup condition for this character state is ovipositor largely membranous (Fig. 8.1E).

6 Abdomen posterior to tergite 7 withdrawn into segment 7 in female (Fig. 8.1C-D).

7 Abdominal constriction in female posterior to tergite 4 (Brown *et al.*, in press).

8 Tergite 5 and 6 extremely short (Brown *et al.*, in press).

9 Tergite 6 encircles entire segment (Brown *et al.*, in press).

10 Frons with extra seta (Peterson, 1987, Fig. 32).

11 Apical foretarsomere narrowed, elongate.

This character state is subject to extensive homoplasy.

12 Tergite 7 with separate, posterior sclerite (Brown, 1988, Fig. 109).

13 Distinctive, hook-shaped seta present on venter of female ovipositor (Prado, 1976, Figs. 64-66).

8.9 Classification

All taxa are *sedis mutabilis*.

MEGASELIA-GROUP

Pericyclocera Schmitz
Trophithauma Schmitz
Megaselia Rondani, in part
Gymnophora-subgroup
    Gymnophora Macquart
    Woodiphora Schmitz
    Megaselia Rondani, in part

Apocephalus-subgroup
  - *Diocophora* Borgmeier
  - *Kerophora* Brown
  - *Myriophora* Brown
  - *Phalacrotophora*-series
    - *Phalacrotophora* Enderlein
    - *Rhyncophoromyia* Malloch
    - *Physoptera* Borgmeier
  - *Apocephalus*-series (included taxa listed below)

Included Nearctic Region genera. ***Apocephalus*** Coquillett, ***Diocophora*** Borgmeier, *Gymnophora* Macquart, ***Kerophora*** Brown, ***Megaselia*** Rondani, ***Myriophora*** gen. n., *Pericyclocera* Schmitz, ***Phalacrotophora*** Enderlein, ***Physoptera*** Borgmeier, *Rhyncophoromyia* Malloch, ***Trophithauma*** Schmitz, ***Woodiphora*** Schmitz.

Notes on included genera. Besides the genera listed by Disney (1989a), females of the genera *Johowia* Silva Figueroa (not Nearctic), ***Kerophora***, ***Physoptera*** and *Trophithauma* have a Dufour's mechanism and are thus undoubted members of this group.

8.10 Revision of genera

Unassigned taxa and *Megaselia*

8.10.1 *Pericyclocera* Schmitz 1927a

Type species: *Pericyclocera molliventris* Schmitz 1927a (original designation).

Derivation of generic name. This name is derived from Greek, and loosely translated means "encircling the antennae." It refers to the produced lower facial margin that nearly touches the lower margin of the frons, producing an enclosed antennal cavity.

Diagnosis. Lower facial margin enlarged, upturned.

Way of life and immature stages. The members of this genus exhibit divergent life histories. Of the two Nearctic Region species, *P. cata* was collected near the burrows of Halictidae (Hymenoptera) (Melander & Brues, 1903) but no definite host-parasite, or other, relationship was observed, whereas *P. floricola* was collected from flowers (Borgmeier, 1966). Adults of *P. arachnophila* Borgmeier (Brazil) inhabit the burrows of the spider *Trechona venosa* (Latreille) (Bristowe, 1925), and *P. diptychogastra* Schmitz (Africa) is also associated with spiders (Schmitz, 1940). Two species from the Neotropical Region were collected on, and suspected of pollinating, tropical grasses of the genus *Pariana* (Soderstrom & Calderón, 1971). Finally, *P. javicola* Beyer (Java) was bred from snails (Beyer, 1959).

Collecting methods. I have collected only one specimen of this genus, with a Malaise trap.

Geographic distribution. Found worldwide.

Phylogenetic relationships. Unknown. The species of this genus need to be studied closely.

Hypothesized autapotypic character states of *Pericyclocera* include the following:

1 Lower facial margin enlarged, upturned.

Number of recognized species. Total of six; two are found in the Nearctic Region.

Material examined. ***Pericylocera*** **undescribed species**, 1 female, ECUADOR: Pichincha: 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown and L.Coote, Malaise trap, rain forest, 180m (BVB).

8.10.2 *Trophithauma* Schmitz 1925

Type species: *Trophithauma portentum* Schmitz 1925 (original designation).

Derivation of generic name. This name is derived from two Greek words for "wonderful feeder", refering to the remarkable, modified mouthparts found in adult female specimens of this genus.

Diagnosis. Female with modified mouthparts, male like *Megaselia* (according to Borgmeier, 1963; Gotô, 1984).

Way of life and immature stages. Unknown. *T. rostratum* has been collected near halictid bee burrows (Melander & Brues, 1903).

Collecting methods. Rarely collected in Malaise traps. Gotô (1984) found *T. fulvum* Gotô to be collected easily in Japan by sweeping herbaceous vegetation in deciduous forests.

Geographic distribution. Specimens of this genus are known from the Nearctic, Neotropical, Palearctic and Oriental Regions.

Phylogenetic relationships. Unknown.

Hypothesized autapotypic character states of *Trophithauma* include the following:

1 Mouthparts of female markedly modified, projected; clypeus elongate, enlarged (see Gotô, 1984, Figs. 1A-B).

2 Abdomen of female modified (Gotô, 1984) with various papillae, and modified sclerites.

Number of recognized species. Total of five; one is found in the Nearctic Region.

Nearctic Region material examined. ***T. rostratum*** **(Melander and Brues)**, CANADA: Ontario: 1♀, 3km W Puslinch, Crieff Bog, 20-26.vi.1987, D.Blades, forest edge/ hummock, pan trap (BVB).

Material examined from other zoogeographic regions. ***Trophithauma*** **spp**, ECUADOR: Napo: 1♀, 5km N El Chaco, 15.ii.1983, M.Sharkey, Malaise trap (BVB), VENEZUELA: Lara: 3♀, Yacambú, 1200m, 7.v.1981, H.Townes, Malaise trap (BVB).

8.10.3 *Megaselia* Rondani 1856

Type species: *Megaselia crassineura* Rondani 1856 (original designation) = *Phora costalis* Roser 1840

Derivation of generic name. Unknown. This name may refer in some way to the enlarged costa of the type species, or may be an euphemistic reference to the size of the wing (*selidos*= page of a book, or sheet of paper).

Notes about synonymy. Disney (1989a) has shown that this genus is paraphyletic with respect to other, recognized genera. Myriads of species have been placed in ***Megaselia***, most of which apparently have not diverged markedly in structure from the groundplan of the *Megaselia*-group. The assignment of the species classified in *Megaselia* into monophyletic groups is a daunting task, as there are an estimated 5,000 to 20,000 extant species (Disney, 1983).

Diagnosis. Impossible; this is a paraphyletic group. Disney (1981) provided the most recent attempt to characterize this grade group.

Way of life and immature stages. Ferrar (1987) summarized the known information for the genus *Megaselia*; in short, they are the most varied group of Phoridae in life history traits, ranging from phytophages, saprophages, predators, to parasitoids. Immatures of several species have been described (references in Ferrar, 1987).

Collecting methods. Some species are among the most easily collected phorids, and are often overwhelmingly abundant in Malaise, pan and flight intercept trap collections. All collecting methods will gather a large variety of species, especially Malaise traps with pans underneath the central baffle, as proposed by Marshall (1982). Rarely collected species are sometimes reared from mushrooms.

Fossils. Fossil *Megaselia* are known from Baltic amber (Brues, 1915, 1939), Dominican amber (Disney, 1987), Zanzibar copal (Brues, 1915), and Eocene Fushun amber (Hong, 1981).

Geographic distribution. Worldwide.

Phylogenetic relationships. Some species of *Megaselia* belong in a monophyletic group with the genera *Gymnophora* and *Woodiphora.* This group has males with the character state notopleural cleft present (Disney, 1989a), and includes, besides *Gymnophora* and *Woodiphora,* at least *M. albicans* (Wood), *M. giraudii* (Egger), *M. malhamensis* Disney and *M. parnassia* Disney (all *M. Megaselia* Group VI). These species should be revised and new generic names applied.

Number of recognized species. Over 1,500.

Material examined. I examined specimens of many unidentified species from the Nearctic, Neotropical and Palearctic Regions.

***Gymnophora*-subgroup**

Diagnosis. Thorax of male with notopleural cleft (Fig. 8.1A).

Geographical distribution. Worldwide.

Phylogenetic relationships. Unknown.

Included genera. Gymnophora Macquart, *Woodiphora* Schmitz, some species of *Megaselia* Rondani. According to Disney (1989b) the included species of *Megaselia* are at least *M. albicans* (Wood), *M. giraudii* (Egger), *M. malhamensis* Disney and *M. parnassia* Disney. These *Megaselia* species should be revised to see if they form one or more monophyletic group; this group, or groups, would require a new generic name.

8.10.4 *Gymnophora* Macquart 1835

Type species: *Phora arcuata* Meigen 1830 (monotypy)

Derivation of generic name. This name is derived from the Greek word for bare, referring to the reduced body setation.

Diagnosis. Both male and female with notopleural cleft. Male terminalia de-rotated 90 degrees. Radial veins swollen. Setae of entire body short. Frons with anterior lobe.

Way of life and immature stages. Baumann (1979) believed that adult females of this genus followed dying slugs (Mollusca: Pulmonata) into the soil and parasitized them. This was sheer speculation, however, based on three factors: 1) a single collection of a female *G. quartomollis* Schmitz on a slug, 2) the relatively few female *Gymnophora* collected from emergence traps in his study, and 3) the large number of slugs present at the study site. My own rearings (Brown, 1987b, unpublished data) show that whereas slugs are indeed a suitable medium for larval development, female *G. luteiventris* Schmitz only oviposited on slugs that had started decomposing and were in a semi-liquid state. Subsequently, I have reared *G. arcuata*, *G. luteiventris* and another, undescribed species from Thailand in the laboratory from dead slugs, dead insects and dead earthworms. W.H. Robinson (personal communication) has reared *G. luteiventris* from rotting potato peels.

Adults of this genus in Canada are most common from late June to mid-August, and are often seen running and mating on undergrowth leaves in deciduous forests. Mating also occurs in flight. Adults mate more than once (Brown, 1985).

The immature stages of *G. luteiventris* were described previously (Brown, 1987b).

Collecting methods. Baumann (1979) collected large numbers of specimens from emergence traps (photoeclectors) in Germany, but most of my specimens were collected in Malaise, yellow pan and flight-intercept traps. Pan traps baited with a dead squirrel in California collected several specimens of *G. talea*.

Geographical distribution. Species of *Gymnophora* are found in the Holarctic, Neotropical and Oriental Regions. A reference to a female from Fiji (Brown, 1987b) was in error; the specimen was actually from Mt. Fiji, Japan.

Phylogenetic relationships. According to Disney (1989a), the genus *Gymnophora*, along with some species of *Megaselia*, is the adelphotaxon of the genus *Woodiphora*.

Hypothesized autapotypic character states of *Gymnophora* include the following:

1 Female with notopleural cleft.

2 Male terminalia de-rotated 90°.

3 Body setae short.

Number of recognized species. Total of fifty-three; six are found in the Nearctic Region.

Material examined. In the course of my revisionary work on this genus (Brown, 1987a, b, 1989), I have examined all except three of the described species of *Gymnophora*. The following records are those of material not included in my earlier works.

Nearctic Region material examined. ***G. carina*** **Brown**, UNITED STATES: Arizona: Cochise Co., 1♀, near Portal, Cave Creek, 25.vii.1986, B.V.Brown, leaf litter, oak forest (BVB), 18.5km W Portal, Basin Trail head, 1♀, 7-10.vi.1986, 2♀, 8-10.vii.1987, yellow pans, B.Brown and T.Spanton, 1950m, oak/ pine/ juniper (BVB), 12.5km S Sierra Vista, Ramsey Canyon, 1♂, 1♀, 11-18.vi, 2♀, 18-25.vi, 1♂, 28.vii.-2.viii, 1♂, 2-8.viii, 1♀, 13-23.viii, 1♀, 15-22.x, 1♀, 22-29.x, 1♀, 7-13.xi.1986, 6♂, 4♀, 9.vii., 2♀, 10.vii.1987, B.V.Brown, Malaise trap, 1700m, oak/ pine/ juniper (BVB) 15♂, 10♀, New Mexico: Catron Co., 2.4km W Luna, 7-8.vii.1987, B.V.Brown, yellow pans, 2300m, oak/ pine/ juniper (BVB), 1♀, Coconino Co., 8km N Humphries Peak, 13-14.vii.1987, B.V.Brown, yellow pans, 2600m (BV.B); ***G. fastigiorum* Schmitz**, CANADA: Alberta: 1♂, 15 km S Beaver Mines, Castle R. Bridge Campground, 23-29.vii.1986, T.G.Spanton, FIT, spruce/ fir (BVB), 1♂, Edmonton, University of Alberta Ecological Reserve, 27.vi.-4.vii.1986, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB), 1♀, 50km SW Nanton, Hailstone Butte, 21.vii.1987, A.T. Finnamore, sweep (BVB), 1♂, 19km W Robb, 6.vii.-9.viii.1986, B.Brown and T.Spanton, FIT, spruce/ larch bog (BVB), 3♂, 1♀, 36km W Robb, Watson Creek Recreation Area, 25-27.vii.1987, B.V.Brown, yellow pans, 1520m, lodgepole pine (BVB), 1♂, British Columbia: Pallister River Basin, 114°25'E, 50°31'N, 5500', 29.vii.1987, G.Pohl, FIT, lodgepole pine forest (BVB); ***G. luteiventris* Schmitz**, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 1♀, 20-27.v, 1♂, 5-14.vii, 2♀, 14-22.vii, 2♂, 1♀, 22.vii, 1♀, 18-25.viii.1986, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB), 1♀, Opal, 53°59'N, 113°13'W, 18-25.viii.1986, B.V.Brown, Malaise trap, sand, jackpine (BVB), UNITED STATES: Connecticut: Tolland Co., Mansfield Center, 1♀, 23.viii-2.ix, 1 ♀ 2-15.ix.1987, J.E.O'Donnell, Malaise trap (BVB); ***G. marshalli* Brown**, 1♂, CANADA: Alberta: 36km W Robb, Watson Creek Recreation Area, 6.vii.-9.viii.1986, B.V.Brown, FIT, 1520m, lodgepole pine (BVB); ***G. subarcuata* Schmitz**, CANADA: Alberta: 6♂, 1♀, 15 km S Beaver Mines, Castle R. Bridge Campground, 23-29.vii.1986, T.G.Spanton, FIT, spruce/ fir (BVB), 2♂, Edmonton, University of Alberta Ecological Reserve, 5-14.vii.1986, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB), Opal, 53°59'N, 113°13'W, 1♂, 17-22.vii, 1♂, 1♀, 17-

23.viii.1986, B.V.Brown, Malaise trap, sand, jackpine (BVB), British Columbia: 1♀, Mt Robson Provincial Park, 5.vii-10.viii.1986, B.Brown and T.Spanton, 850m, FIT, cedar/ aspen/ pine (BVB), UNITED STATES: 1♂, 1♀, Alaska: 18 mi S Delta Junction, Sawmill Creek, mi 1339 AK Highway, 26.vii.1986, B.V.Brown, spruce forest (BVB); Washington: 1♀, Chelan Co., 13km SW Leavenworth, 8-Mile Campground, 28-29.vi.1987, Malaise trap, B.V.Brown (BVB), 2♂, Gray's Harbour Co., Humptulips, 23.vi.1987, B.V.Brown, on muddy path, 2nd growth deciduous forest (BVB), Jefferson Co., Olympic National Park, 8♂, 4♀, Queets River Road, 1♂, Quinalt Lake Road, 22-24.vi.1987, B.V.Brown, Malaise trap, rain forest (BVB), 1♀, Lewis Co., Mt Rainier National Park, Ohanapecosh, 26-27.v.1987, 670m, B.V.Brown, Malaise trap, Douglas fir/ hemlock/ cedar (BVB), 2♂, 6♀, Whatcom Co., 8km S Bellingham, 1.vi-3.vii.1986, B.Brown and T.Spanton, FIT, cedar/ aspen (BVB); ***G. talea* Brown**, UNITED STATES: California: Shasta Co., 25♂, 2♀, 64km N Redding, 600m, 3-30.vi.1986, FIT, B.Brown and T.Spanton, pine/ spruce/ cedar/ oak (BVB), 1♀, 25km W Redding, 27-30.vi.1986, B.Brown and T.Spanton, Malaise trap, oak forest (BVB), 10♂, 4♀, Tuolumne Co., 1.5km E. Tuolumne, 15-26.vi.1986, 750m, B.V.Brown and T.G.Spanton, Malaise trap, FIT, carrion trap, oak foothill forest (BVB).

Material from other zoogeographic regions. ***G. cymatoneura* Enderlein**, COSTA RICA: Puntarenas: Monteverde, Finca Canada, 1700m, 1♂, 28.v.-1.vi., 1♂, 1-5.vi.1988, clearcut/ cloud forest, 1♂, 28.v.-1.vi.1988, stunted forest, B.V.Brown, Malaise trap (BVB); ***G. spiracularis* Borgmeier**, ECUADOR: Napo: Tena, 3♂, 22-27.v.1987, 500m, B.Brown and L.Coote, Malaise trap, 2nd growth forest (BVB), Pichincha: 1♂, 17km E Santo Domingo, above Tinalandia, 9-13.v.1987, B.Brown and L.Coote, Malaise trap, montane forest (BVB), GUATEMALA: Zacapa: 2♂, 1♀, San Lorenzo, 2300m, 13-17.xi.1986, M.Sharkey, Malaise trap, cloud forest (BVB); ***Gymnophora* sp.1**, THAILAND: 70km SW Chiang Mai, Doi Inthanon National Park, 7.ii.1989, T.W.Thormin, 1570m, wet, evergreen forest, pan trap (BVB); ***Gymnophora* sp.2**, 2♂, THAILAND: 70km SW Chiang Mai, Doi Inthanon National Park, 2200m, 6-12.v.1990, B.V.Brown, Malaise trap, oak forest (BVB).

8.10.5 *Woodiphora* Schmitz 1926b

Type species: *Phora retroversa* Wood 1908 (original designation)

Derivation of generic name. This genus is named for the Dipterist J.H.Wood, who described the type species.

Diagnosis. Dufour's mechanism in female with dark, dumbell-shaped inner region, outer region lightly pigmented; with anterior pair of blindly ending tubules that loop below rest of mechanism and extend into crop.

Way of life and immature stages. Unknown. Disney (1985) noted that adults are attracted to crushed termites in Sulawesi, apparently feeding on their body fluids.

Disney also noted (1989a) that individuals of one species had large numbers of fungal spores in their crops, and that another species was attracted to concentrations of ants.

Collecting methods. These flies are frequently collected in Malaise traps.

Geographic distribution. Species of this genus are found Worldwide.

Phylogenetic relationships. This genus belongs in an unresolved monophyletic group with *Gymnophora* and some species of *Megaselia*.

Hypothesized autapotypic character states of *Woodiphora* include the following:

1 Dufour's mechanism of female dumbell-shaped.

Number of recognized species. Total of forty-one; one is found in the Nearctic Region.

Nearctic Region material examined. No specimens from the Nearctic Region were examined.

Material examined from other zoogeographic regions. **W. magnipalpis (Aldrich),** HONDURAS: 1♂, Roatan I. (west), 1.i.1980, G.E.Bohart (BVB), MEXICO: Jalisco: 1♂, Chamela, 26.ix.-8.x.1985, Parker and Griswold (BVB), WEST INDIES: St. Kitts: 4♂, Mt. Misery, 730m, 4-20.xii.1985, L.D.Coote, rain forest, crater rim (BVB).

Apocephalus-subgroup

Diagnosis. Paired sternite 8 elongate.

Geographical distribution. Worldwide.

Phylogenetic relationships. Unknown.

Included genera. *Apocephalus*-series genera (see below), plus *Diocophora* Borgmeier, *Kerophora* Brown, *Myriophora* gen. n.,

Unassigned *Apocephalus*-subgroup taxa

8.10.6 *Diocophora* Borgmeier 1959

Type species: *Diocophora disparifrons* Borgmeier 1959 (original designation).

Derivation of generic name. According to Borgmeier (1959) this name refers to the Greek *diókein*, meaning to pursue or persecute.

Diagnosis. Male with enlarged, deep cercus.

Way of life and immature stages. Two of these flies were collected with ants in Brazil: *D. disparifrons* Borgmeier attacking *Camponotus rufipes* and *C. cingulatus*, and *D. appretiata* Schmitz with *Eciton burchelli* (Westwood) and *E. quadriglume* Haliday. Rettenmeyer and Akre (1968) found *D. appretiata* in the raiding columns and refuse deposits of *E. burchelli* Disney and Kistner (Disney & Kistner, 1989) also reported D. *appretiata* with *E. burchelli.* I have observed *D. appretiata* associated with *E. burchelli* at the La Selva Biological Station, Puerto Viejo de la Sarapiqui, Heredia Province, Costa Rica and the Rio Palenque Science Center, Pichincha Province, Ecuador. In both localities adults of both sexes of the flies were frequently seen perched on leaves and overhanging plants, or hovering over the ants. The flies were associated with the diurnal raiding columns, and were not seen associated with the swarm front, where a different group of phorid flies, mainly species of *Apocephalus* and *Acanthophorides*, predominates. Instead, these flies are associated with the columns of workers going toward and returning from the swarm front. During several hours of observation of columns of *E. burchelli* at La Selva, only one presumed attack occurred. In this instance, a female that was perched on a leaf near the column suddenly flew over the ants and darted at a booty-laden, large worker. Apparently, no successful oviposition took place. Other individuals were watched for several minutes each, but no other attacks occurred.

A new, and first North American, host record is *Diocophora trichogaster* parasitizing the ant *Camponotus floridanus.* These flies were reared from and collected with their ant hosts in Florida. One specimen is labelled "riding on the head of" the host ant.

The immature stages are undescribed.

Collecting methods. Although these flies are occasionally collected in Malaise traps, it is preferable to catch and observe them with their hosts. *D. appretieta* is found easily beside army ant columns and can be collected individually with an aspirator. Other species may be collected by baiting their host ants that, in at least two instances, are species of *Camponotus.*

Geographic distribution. These flies are found in the Nearctic and Neotropical Regions.

Phylogenetic relationships. Unknown. This genus may be the adelphotaxon of *Myriophora* as some females of both genera have unusual, flat spinuli on the ovipositor.

Disney and Kistner (1989) have expressed doubt about the monophyly of this genus. This uncertainty is based on the possession at least one of the diagnostic characters of *Diocophora* in some species of *Megaselia*, and the possession of supposedly primitive character states in *Diocophora*, such as Dufour's mechanism in females, male tergite 10 and a bi-articled palpus. They implied that if greater justification for this genus was not found, it would have to be subsumed within the genus *Megaselia.* As discussed earlier, however, I interpret the structure Disney refers to as tergite 10 in *Diplonevra* as a neomorphic character state. This structure is different in *Diocophora*, as there is no clear division between the cercus and the so-called tergite 10, rather the two structures merge into each other. The line of division between tergite 10 and cercus in Disney and Kistner (1989, Fig. 15) is in fact not a division, but a steep slope. The structure refered to as a surstylus is a spinose ventromedial process that may not be homologous with a surstylus. This process is not present in other species I have examined. The so-called tergite 10 in found in some other species of this genus, but its development is various, and most obvious in those species showing obvious development of other so-called *Diocophora* character states, such as male flagellomere 1 enlarged, and male cercus compressed. I believe this tergite 10 in *Diocophora* is in fact a basal swelling of the cercus, or possibly another neomorphic structure separated from the epandrium as in *Diplonevra*.

The synonymy of this genus with *Megaselia*, as proposed by Disney and Kistner (1989) would serve no useful purpose in my opinion, because *Megaselia* has already been shown to be a paraphyletic genus (Disney, 1989a) and because there is evidence to link *Diocophora* species with other *Apocephalus*-subgroup genera. See also under "Phylogenetic relationships" for *Megaselia*.

Number of recognized species. Total of ten; two are found in the Nearctic Region.

Nearctic Region material examined. ***D. trichogaster*** **Borgmeier**, UNITED STATES: Florida: 2♂, 2♀, Alachua Co., about 6.5mi SW Gainesville, Greenleaf Subdivision, 1.vii. 1987, R.K. Vander Meer, reared from bodies of *Camponotus floridanus* workers, 1♂, 1♀, found riding on head of *Camponotus floridanus* worker (BVB); *Diocophora* sp.1, UNITED STATES: New Mexico: 1♂, Guadalupe Co., Santa Rosa Lake State Park, 3.viii.1984, desert, B.V.Brown, blacklight (BVB); *Diocophora* sp. 2, UNITED STATES: California: 2♂, Tuolumne Co., 6km NE Tuolumne, River Ranch Campground, 22-26.vi.1986, B.V.Brown, Malaise trap, oak forest/ field, 750m (BVB).

Material examined from other zoogeographic regions. ***D. appretiata*** **Schmitz**, COSTA RICA: Heredia: 5♂, 14♀, Puerto Viejo de la Sarapiquí, La Selva Biological Station, 14.v.1989, B.V.Brown, SURA 300, over *Eciton burchelli* (BVB), ECUADOR: Pichincha, 8♂, 5♀, Rio Palenque Science Center, 5.v.1987, B.V.Brown, *Eciton burcelli* raiding column, 180m, rain forest (BVB); ***Diocophora*** **sp. 3**, ECUADOR: Napo: 1♂, 10km SW Puerto Napo, Limón Chicta, 23-27.v.1987, B.Brown and L.Coote, 600m, Malaise trap, rain forest (BVB); ***Diocophora*** **sp.4**, VENEZUELA: 2♂, Zulia, 200m, 20-23.iv.1981, Townes and Masner, Malaise trap, rain forest (BVB).

8.10.7 *Kerophora* Brown 1988

Type species: *Kerophora ferruginea* Brown 1988 (original designation).

Derivation of generic name. This name is derived from Ker, a Greek goddess of death.

Diagnosis. Epandrium with anteroventral concavity. Female terminalia distinctive, segments 8-10 forming long, dorsally-curved stylet, cerci ventral.

Way of life and immature stages. According to Disney (personal communication), *K. brunnea* is a parasitoid of a scale insect.

Immature stages are not known.

Collecting methods. So far, I have collected specimens of this genus only with Malaise traps.

Geographic distribution. These flies are still known only from their type localities: Edmonton, Alberta (*K. brunnea* and *K. ferruginea*) and Great Falls, Virginia (*K. sicula*)

Phylogenetic relationships. Unknown.

Hypothesized autapotypic character states of *Kerophora* include the following:

1 Distinctive stylet of female ovipositor.

2 Cerci ventral on female ovipositor.

3 Male epandrium with lateral concavity.

Number of recognized species. Total of three.

Nearctic Region material examined. Type material of ***K. brunnea*** **Brown**, ***K.***

ferruginea Brown, and ***K. sicula*** **Brown** was examined previously (1988). Further records are as follows: ***K. brunnea*** **Brown**, 19♂, 10♀, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 3-10.v.1988, B.V.Brown, Malaise trap, spruce/ poplar/ aspen (BVB); ***K. ferruginea*** **Brown**, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 8♂, 29.v.-5.vi, 3♀, 5-12.vi.1986, 2♂, 3-10.v, 2♂, 18-25.v.1988, B.V.Brown, Malaise trap, spruce/ poplar/ aspen (BVB).

8.10.8 *Myriophora* gen. n.

Type species: *Plastophora juli* Brues 1908 (present designation).

Derivation of generic name. This name is derived from Myriapoda, the name for centipedes and millipedes that are the victims of these parasites.

Notes about synonymy. This genus contains some of the species formerly classified in the genus *Plastophora* Brues (1905). The concept of *Plastophora* became obscured with widening of the generic diagnosis and loss of the holotype of the type species, *P. beirne* Brues. Disney (1978, 1986) synonymized *Plastophora* with *Megaselia*, citing the lack of distinctive character states that separated the two genera. According to Disney (1978), a series of intermediates exist between *Megaselia* and *Plastophora* in the major character states defining the latter genus, including the elongate ovipositor. Such concerns about taxa grading into *Megaselia*, however, are irrelevant when

Megaselia itself is known to be paraphyletic (as demonstrated by Disney, 1989a). With this revision of the *Megaselia*-group, it is clear that some former species of *Plastophora* are more closely related to (in other words share more synapotypic character states with) other parasitic genera such as *Diocophora*, *Kerophora*, etc., than to other species of *Megaselia*. Thus, based on close examination of the structure of female specimens, this group deserves generic status.

It is impossible to say which species of the former genus *Plastophora* belong in *Myriophora* without examining examples of each species. Certainly species with a distinctive epandrial notch (Disney, 1978, Figs. 2,3) belong here, including *M. audreyae* (Disney) **comb. n.**, *M. elongata* (Wood) **comb. n.**, *M. equitans* (Schmitz) **comb. n.**, *M. juli* (Brues) **comb. n.** and several undescribed species in my collection from the Neotropical, Nearctic and Oriental regions. Species that probably do not belong here, but which formerly were classified as *Plastophora* include *Megaselia chainensis* Disney, *M. submarginalis* (Malloch) and *M. winnemana* (Malloch) (personal observation), as well as *Megaselia emarginata* (Wood), *M. luteipes* (Schmitz), *M. rufa* (Wood), *M. spinigera* (Wood), and *M. styloprocta* (Schmitz), all of which lack the epandrial notch (Disney, personal communication).

Diagnosis. Dufour's mechanism present in females of some species only. Female ovipositor markedly strigulate, markedly compressed; abdominal segment 7 with extremely elongate tergite and sternite, downturned at tip; sternite 8 elongate; cerci large, pointed ventrally and withdrawn into body at rest, cercal setae greatly reduced.

Male of one species, *M. juli* (Brues), with unusual large swelling of vas deferens posterior to looping over hindgut. Males of undoubted *Myriophora* species with distinctive notch on both sides of epandrium.

Way of life, immature stages, and collecting methods. These flies are parasitoids, many of which attack myriapods (Banks, 1911; Berland, 1932; Disney, 1978; Knab, 1913; Picard, 1930; Schmitz, 1939b). Some species classified in the genus *Plastophora* were known to attack other hosts, but such records cannot be carried over into this new genus without examining each phorid species individually for the diagnostic character states of *Myriophora*.

One account of phorids attacking myriapods specified that only injured hosts are attacked (Berland, 1932), so I attempted to artificially wound some of these arthropods to see if they provide a strong attractant for the flies. In Khao Yai National Park, Thailand, I chopped millipedes of two different species (families Platyrhacidae and Harpagophoridae) into pieces for bait and collected numerous male and female specimens of a *Myriophora* species. One female confined in a vial with a piece of dead millipede laid an egg, and a single female specimen was reared. No larval specimens are known. Undoubtedly, this technique of collecting and rearing could be used in other, less exotic, locations.

Geographical distribution. Found at least in the Holarctic, Afrotropical, Neotropical and Oriental Regions.

Phylogenetic relationships. The exact relationships of this genus are unknown, but it belongs in the *Apocephalus*-group of genera.

Hypothesized autapotypic character states of *Myriophora* include the following:

1 Male epandrium with distinctive notch.

2 Female cerci withdrawn into terminalia at rest (Fig. 8.1F).

3 Tip of female terminalia downturned (Fig. 8.1F, 8.4).

Number of recognized species. Four.

Material examined. ***M. juli*** **(Brues)**, CANADA: Ontario, Guelph, South Arboretum, 32 ♂ and ♀ specimens from 11.vi. to 11.ix.1984-1985, B.V.Brown, Malaise trap, flight intercept traps, deciduous forest (BVB), UNITED STATES: 1♀, Indiana, Owen Co., Lieber State Park, 30.viii.1984, B.V.Brown, deciduous forest (BVB), 1♀, Texas, Travis Co., Austin, Brackenridge Field Laboratory, 28.x.1988, A.Hook, Bio.No. 60-88, attacking Parajulidae (BVB).

Also, I examined numerous unidentified specimens from Canada, Costa Rica, Ecuador, Guatemala, Mexico, Panama, Peru, Thailand, United States, Venezuela, and the West Indies (Nevis).

Phalacrotophora-series

Diagnosis. Venter of female segment 8 deeply cleft (Figs. 8.5A-C).

Geographical distribution. Worldwide.

Phylogenetic relationships. Unknown.

Included genera. Phalacrotophora Enderlein, *Physoptera* Borgmeier, and *Rhycophoromyia* Malloch.

8.10.9 ***Phalacrotophora* Enderlein 1912**

Type species: *Phalacrotophora bruesiana* Enderlein 1912 (original designation)

Derivation of generic name. From the Greek word *phalakros*, meaning bald-headed or smooth, referring to the glabrous, shiny frons in the type species.

Diagnosis. Eye large, frons narrow, shiny in many species. Hind tibia with anterodorsal setal row. Female with sclerotized ovipositor.

Way of life. The members of this genus exhibit divergent life histories. Of the Nearctic Region species, larvae of *P. epeirae* eat spider eggs (Brues, 1902, plus other references in Ferrar, 1987), *P. halictorum* is associated with halictid bee nests

(Melander & Brues, 1903, plus other references in Ferrar, 1987), and *P. longifrons* is associated with wasps of the families Sphecidae and Siricidae (Borgmeier, 1963). Immatures of *P. fasciata* (Fallén) (Europe), *P. nedae* (Malloch) (Neotropical Region), *P. quadrimaculata* Schmitz (South-East Asia) and *P. berolinensis* Schmitz (Europe) are parasitoids of immature ladybird beetles (Coleoptera: Coccinellidae) (Borgmeier, 1963; Colyer, 1952a, 1954a; Disney, 1990). *P. pruinosa* Borgmeier (Neotropical Region) was recorded as a parasitoid of a wasp (Hymenoptera: Eumenidae) (Borgmeier, 1934).

Certainly the large eyes of the adult females indicate that they are parasitoids, similar to the large-eyed, visually-oriented parasitoids *Neodohrniphora curvinervis* Malloch (Feener and Brown in preparation).

Colyer (1952a) described the puparia of *P. berolinesis* and *P. fasciata*.

Collecting methods. Specimens of *Phalacrotophora* are occasionally collected in Malaise traps, but more interesting data can be obtained by collecting them from their hosts.

Geographical distribution. Worldwide.

Phylogenetic relationships. This genus is part of an unresolved group with *Physoptera* and *Rhycophoromyia*.

Hypothesized autapotypic character states of *Phalacrotophora* include the following:

1 Hind tibia with anterodorsal row of setae.

Number of recognized species. Total of forty-nine; three are found in the Nearctic Region.

Nearctic Region material examined. ***P. epeirae* (Brues)**, CANADA: Alberta: Edmonton, University of Alberta Ecological Reserve, 1♀, 29.v.-5.vi., 1♂, 5-12.vi.1986, B.V.Brown, Malaise trap, spruce/ poplar/ alder (BVB), Ontario: Guelph, South Arboretum, 1♂, 1♀, 22.vii.-6.viii., 1♂, 14-19.viii.1985, B.V.Brown, Malaise trap at forest edge, Malaise trap in deciduous forest (BVB), 1♂, Leamington, Point Pelee National Park, 17.vii.1983, K.Barber, Northwest Beach Trail (BVB), 6♂, 1♀, Long Point Provincial Park, 30.vii.-5.viii.1983, L.Carlson and S.Marshall, Malaise trap (BVB), 1♂, Ottawa, 21.viii.1974, J.R.Vockeroth (BRC), 2♀, Edward Co., Outlet Beach, Pr., 14.viii.1968, J.R.Vockeroth (BRC), UNITED STATES: Missouri: 1♀, Williamsville, 14.vii.1969, Malaise trap (BRC), Pennsylvania: 1♂, Lackawanna Co., Scranton, 12.vi.1985, B.V.Brown, deciduous forest (BVB); ***P. halictorum* (Melander and Brues)**, UNITED STATES: Arizona: 1♂, Cochise Co., near Portal, between Herb Martyr and SWRS, 17.viii.1984, B.V.Brown, sweeping (BVB), 1♂, 1♀, 12.5km S Sierra Vista, Ramsey Canyon, 10,22.vi.1987, B.V.Brown, Malaise trap, 1700m, oak/ pine/ juniper (BVB), 3♂, Yavapai Co., Congress, 23-26.iv.1967, D.M.Wood (BRC), California: 7♂, Riverside Co., University of California, 7-21.vi.1983, D.Yu, Malaise trap (BVB), Shasta Co., 2♂, 1♀, 25km W Redding, 27-30.vi.1986, 450m, B.Brown and T.Spanton, oak forest, Malaise trap (BVB); ***P. longifrons*** **(Brues)**, CANADA: New Brunswick: Kouchibouguac National Park, 9.vii.1977, J.F.McAlpine, code 6024R (BRC), Ontario: Guelph, South Arboretum, 1♂, 21-25.vii.1984, 1♂, 30.v.-5.vi., 1♂, 19-24.vi., 3♂, 1♀, 28.vi.-3.vii., 1♀, 3-9.vii., 2♂, 9-13.vii., 1♂, 13-22.vii., 1♂, 1♀, 22.vii-6.viii., 1♂, 27.viii-4.ix., 1♂, 4-11.ix.1985, UNITED STATES: Arizona: 2♂, Cochise Co., 12.5km S Sierra Vista, Ramsey Canyon, 6,10.vi.1987, B.V.Brown, Malaise trap, 1700m, oak/ pine/ juniper (BVB).

Material examined from other zoogeographic regions. ***P. berolinensis*** **Schmitz**, ENGLAND: Devon: Torquay, 1♂, 4♀, 12.vi., 7♀, 19.vi, 2♀ 20.vi.1960, J.R.Vockeroth (BRC,BVB), SWITZERLAND: Seegraeben, 7.vi.1951, coll. Delucchi (BRC). Other, unidentified, species were examined from Brazil, Ecuador, Nepal, Peru and Uganda (all BRC).

8.10.10 *Rhyncophoromyia* Malloch 1923

Type species: *Rhyncophoromyia trivittata* Malloch 1923 (original designation)

Derivation of generic name. This name is derived from the Greek word for nose or snout, referring to the elongate proboscis in the female.

Diagnosis. Female with elongate proboscis. Female terminalia partly sclerotized. Male with cercus elongate.

Way of life and immature stages. In the original description of *R. conica* (Malloch, 1912), this fly was noted to be a parasitoid of *Camponotus pennsylvanicus* (DeGeer) (Hymenoptera: Formicidae). Two unidentified species of this genus were collected over *Camponotus abdominalis* (F.) and *C. femoratus* (F.), in Panama and Ecuador, respectively.

The immature stages of all species are unknown.

Collecting methods. These flies are occassionally collected in Malaise traps, but specimens collected by baiting host ants are more useful.

Geographical distribution. These flies are known only from the Nearctic and Neotropical Regions, but I have seen specimens from Sumatra, Indonesia also.

Phylogenetic relationships. This genus is part of the unresolved group including *Phalacrotophora* and *Physoptera*.

Hypothesized autapotypic character states of *Rhycophoromyia* include the following:

1 Female proboscis long.

2 Tergite 6 of male shiny.

Number of recognized species. Total of ten; two are found in the Nearctic Region.

Nearctic Region material examined. ***R. conica*** **(Malloch)**, CANADA: Ontario: 1♂, Foote's Bay, shore of Lake Joseph, 11-30.viii.1985, B.V.Brown, Malaise trap, 2nd growth deciduous forest (BVB), Guelph, South Arboretum, 1♀, 24-30.v., 1♂, 30.v.-5.vi., 1♀, 22-28.vi., 2♂, 1♀, 28.vi.-3.vii., 1♀, 3-9.vii., 1♀, 9-13.vii.1985, B.V.Brown, Malaise trap at forest edge (BVB), UNITED STATES: Missouri: Laclede Co., Bennett Springs State Park, 1-2.viii.1984, B.V.Brown, water [pan] traps (BVB).

Material examined from other zoogeographic regions. Eighteen specimens of Neotropical Region *Rhyncophoromyia* are in my collection, but because there are many new species among them, they cannot be accurately identified at this time. These specimens are from Costa Rica, Ecuador, Mexico, Panama, Peru, and Venezuela.

8.10.11 *Physoptera* Borgmeier 1958,

Type species: *Aphiochaeta vesiculata* Borgmeier 1925 (original designation)

Derivation of generic name. This name is derived from the Greek *physa* for bubble, referring to the swelling in the wing of females.

Diagnosis. Female with swelling at base of wing. Male with swollen fore metatarsus.

Way of life and immature stages. Unknown.

Collecting methods. I have collected specimens of this genus only with Malaise traps.

Geographic distribution. Neotropical and Nearctic Regions. I have seen male phorids from Ibadan, Nigeria, that have the same swollen foretarsomere as in male *Physoptera*, but no corresponding females were present.

Phylogenetic relationships. The female of this genus has a Dufour's mechanism (Fig. 8.2J), making this an undoubted member of the *Megaselia*-group of genera. It is part of the unresolved group including *Phalacrotophora* and *Rhyncophoromyia*.

Hypothesized autapotypic character states of *Physoptera* include the following:

1 Female with swelling at base of wing.

2 Male with swollen fore metatarsus.

Number of recognized species. Total of thirteen; two are found in the Nearctic Region.

Material examined. I saw no specimens of the two Nearctic Region species, *P. apicinebula* (Malloch), and *P. parastigmatica* Borgmeier.

Other material examined was as follows: ***P. membranosa* Borgmeier**, COSTA

RICA: Puntarenas: 1♀, Monteverde, 1700m, 1-5.vi.1988, Malaise trap, B.V.Brown, stunted forest (BVB); ***P. pictiventris* Borgmeier**, COSTA RICA: Heredia: 1♀, La Selva Biological Station, 40m, 23-26.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50 (BVB); ***P. pleurospinosa* Borgmeier**, ECUADOR: Pichincha: 1♀, 17km E Santo Domingo, Tinalandia, 6-13.v.1987, B.V.Brown, 710m, clubhouse windows (BVB); ***Physoptera* species 1**, ECUADOR: Napo: 1♀, Tena, 22-27.v.1987, 500m, B.Brown and L.Coote, Malaise trap, 2nd growth forest (BVB).

I also examined five male specimens of different species, none of which, in spite of their co-occurence with identifiable female specimens, could be identified satifactorily with the available key (Borgmeier & Prado, 1975). **male 1**, COSTA RICA: Heredia: La Selva Biological Station, 40m, 23-26.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50 (BVB); **male 2**, COSTA RICA: Heredia: La Selva Biological Station, 40m, 16-23.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50 (BVB); **male 3**, COSTA RICA: Puntarenas: Monteverde, 1700m, 28.v.-1.vi.1988, Malaise trap, B.V.Brown, stunted forest (BVB); **male 4**, COSTA RICA: Heredia: La Selva Biological Station, 40m, 23-26.v.1988, B.V.Brown, Malaise trap, 2° forest, SAT 100 (BVB); **male 5**, ECUADOR: Pichincha: 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown and L.Coote, Malaise trap, rain forest, 180m (BVB).

Apocephalus-series

Diagnosis. Female segment 7 modified for parasitism, as a prying mechanism to lift host sclerites, or in some other way to facilitate egg deposition. Segments posterior to segment 7 withdrawn into segment 7 at rest. Possibly also only 2 rectal papillae present (as in *Apocephalus* and *Lecanocerus*)

Geographical distribution. Worldwide.

Phylogenetic relationships. Unknown.

Adelphotaxa within the *Apocephalus*-series include *Menozziola* + *Trucidophora*, *Cremersia* + *Neodohrniphora*, *Pseudacteon* + (at least New World) *Microselia*, *Dacnophora* + *Myrmosicarius*. *Lecanocerus* apparently is a relatively plesiotypic genus in this series, as the stylet formed by segments 8-10 is not as elongate in the female of *L. compressiceps* as in other included taxa.

Included genera. *Apocephalus* Coquillett, *Auxanommatidia* Borgmeier, *Cremersia* Schmitz, *Dacnophora* Borgmeier, *Lecanocerus* Borgmeier, *Menozziola* Schmitz, *Microselia* Schmitz, *Myrmosicarius* Borgmeier, *Neodohrniphora* Malloch, *Pseudacteon* Coquillett, *Trucidophora* Brown, *Zyziphora* Peterson & Robinson.

8.10.12 *Lecanocerus* Borgmeier 1962

Type species: *Lecanocerus compressiceps* Borgmeier 1962 (original designation)

Derivation of generic name. This name is based on the Greek *lekos* for plate, referring to the shape of the male flagellomere 1.

Diagnosis. Male with enormously enlarged flagellomere 1 (Peterson, 1987, Fig. 15). Female with frons short, supra-antennal setae porrect (Peterson, 1987, Fig. 16).

Way of life and immature stages. Based on the sclerotized female terminalia, these flies are parasitoids, but their hosts are unknown.

Collecting methods. These flies can be collected in Malaise, pan and flight-intercept traps.

Geographic distribution. Widespread in North America; also central America.

Phylogenetic relationships. Unknown.

Hypothesized autapotypic character states of *Lecanocerus* include the following:

1 Flagellomere 1 of male enormously enlarged.

2 Supra-antennal setae of female porrect.

Number of recognized species. One, from the Nearctic Region and a second, undescribed species from Central America.

Nearctic Region material examined. ***L. compressiceps*** **Borgmeier**, CANADA: **Alberta**: 1♂, Edmonton, University of Alberta Ecological Reserve, 18-25.viii.1986, B.V.Brown, Malaise trap, spruce/ poplar/ aspen (BVB), 1♂, Opal, 53°59'N, 113°13'W, 17-23.viii.1986, B.V.Brown, Malaise trap, sand, jackpine (BVB), **British Columbia**: 14♂, 1♀, Mt. Robson Provincial Park, 5.vii.-10.viii.1986, B.Brown and T.Spanton, 850m, FIT, cedar/ aspen/ pine (BVB), **Nova Scotia**: 1♂, Cape Breton Highlands National Park, Lone Shieling, 11.vii.1983, A.Borkent, maple forest, Malaise trap (BVB), **Ontario**: Guelph, South Arboretum, 1♂, 9-13.vii., 1♂, 6-10.viii., 1♂, 10-14.viii., 1♀, 14-19.viii., 1♂, 19-27.viii.1985, B.V.Brown, Malaise trap at forest edge, Malaise trap in wet, shrubby meadow, Malaise trap in deciduous forest (BVB), **Quebec**: Camp Fortune, 15-22.ix.1982, J. Denis, Malaise trap (BVB).

Material examined from other zoogeographic regions. ***Lecanocerus*** **sp. 1.**, COSTA RICA: **Puntarenas**: 2♂, Monteverde, 1700m, 1-5.vi.1988, B.V.Brown, Malaise trap, clearcut/ cloud forest (BVB), GUATEMALA: **Zacapa**: 4♂, 1♀, San Lorenzo, 2300m, 13-17.xi.1986, M.Sharkey, Malaise trap, cloud forest (BVB).

8.10.13 *Apocephalus* Coquillett 1901

Type species: *Apocephalus pergandei* Coquillett 1901 (original designation).

Derivation of generic name. Translated from the Greek word roots, this name means "separate head", probably referring to the original description that termed *A. pergandei* the "ant-decapitating fly".

Diagnosis. Lower inter-frontal setae in most species close to mid-line, divergent, otherwise parallel; anepisternum without setae; wing vein R_{2+3} present; female with sclerotized tergite 7 modified for prying open sclerites; anterior margin of tergite 7 internal, sclerotized loop-shaped support.

Way of life and immature stages. All known species are endoparasitoids. Most species attack ants (Hymenoptera: Formicidae) of various genera, including *Acromyrex*, *Aphaenogaster*, *Atta*, *Azteca*, *Camponotus*, *Eciton*, *Iridomyrmex*, *Labidus*, *Neivamyrmex*, *Nomamyrmex*, *Paraponera*, *Pheidole*, and *Solenopsis*; however, one species, *A. antennatus* has been reared from immature fireflies (Coleoptera: Lampyridae) (Mead, 1968), a second species, *A. mortifer*, is a parasitoid of a cantharid beetle (Coleoptera: Cantharidae) (Borgmeier, 1937), and a third species, *A. borealis*, has been reared from a black-widow spider (Araneida: Theridiidae) (Borgmeier, 1963) and vespid wasps (Ennik, 1973). All of the species attacking hosts other than ants are classified in the subgenus *Mesophora* by Borgmeier (1963). The other Neartic Region species of *Mesophora*, *A. wheeleri* was listed as "probably parasitic on *Formica fusca* [Hymenoptera: Formicidae], abundant at the collecting place" (Borgmeier, 1963), but this is pure speculation. The only other species classified in *Mesophora* is *A. limai* Prado (Brazil), but there are no host data known, as the specimens were collected in a

Malaise trap (Prado, 1976).

Observations noting the presence of these flies are common in the literature (for example, Burges, 1979; Janzen & Carroll, 1983; LaBerge, 1953; Pergande, 1901; Rettenmeyer & Akre, 1968), but in-depth studies on their interactions with their ant hosts have been made only recently (Brown & Feener, in press-a; Feener, 1981, 1987, 1988; Feener & Brown, submitted; Feener & Moss, 1990).

Borgmeier (1937) superficially described the larval and puparial stages of *A. mortifer*, and illustrated the puparium. Brown and Feener (in press-b) described the larva and puparium of *A. paraponerae* Borgmeier.

Collecting methods. These flies are collected in Malaise traps, yellow pan traps, or, preferably, on their host ants.

Geographical distribution. Nearly all species are known from the New World; species described from India and Australia probably are not congeneric.

Fossils. One undescibed fossil specimen is in the Dominican amber collection of Brown and Feener (BVB), of approximately late Oligocene or early Miocene age. It resembles modern *A. paraponerae*.

Phylogenetic relationships. Unknown. The monophyly of this genus has not been adequately demonstrated, so autapotypic character states cannot be hypothesized.

Number of recognized species. Total of eighty-seven; twenty-one are found in the Nearctic Region.

Nearctic Region material examined. ***A. analis*** **Borgmeier**, ECUADOR: Pichincha: 2♂, 3♀, 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown and L.Coote, Malaise trap, rain forest, 180m (BVB), 1♂, 17km E Santo Domingo, Tinalandia, 7-10.v.1987, 800m, B.Brown and L.Coote, Malaise trap, rain forest (BVB), 1♀, VENEZUELA: Lara: Yacambú, 1200m, 7.v.1981, H.Townes, Malaise trap (BVB); ***A. antennatus*** **Malloch**, 2♂, 3 ♀ UNITED STATES: Missouri: Laclede Co., Bennett Springs State Park, 1-2.viii.1984, B.V.Brown, water [yellow pan] traps (BVB); ***A. coquilletti*** **Malloch**, 2♂, CANADA: Ontario: Guelph, South Arboretum, 13-22, 22-30.vii.1985, B.V.Brown, Malaise trap, wet, shrubby meadow (BVB); UNITED STATES: 1♀, Missouri: Laclede Co., Bennett Springs State Park, 1-2.viii.1984, B.V.Brown, water [yellow pan] traps (BVB), 1♂, New Hampshire: Strafford Co., 4 mi. W Durham, 9-13.ix.1982, R.M.Reeves, Malaise trap (BVB); ***A. feeneri*** **Disney**, 1♂, 2♀, UNITED STATES: Texas: Hardin Co, 13 km N Silsbee, 20.vii.1977, D.H.Feener, with *Pheidole dentata* (BVB), 10♀, Travis Co., Austin, University of Texas, Brackenridge Field Lab., 10,17,18.vii., 14.ix.1977, D.H.Feener, with *Pheidole dentata* (BVB); ***A. grandipalpis*** **Borgmeier**, 1♀, UNITED STATES: New Mexico: Guadalupe Co., Santa Rosa Lake State Park, 3.viii.1984, desert, B.V.Brown, blacklight (BVB); ***A. mortifer*** Borgmeier, CANADA: 1♀, Ontario: Guelph, South Arboretum, 13-17.vii.1984, B.V.Brown, Malaise trap, forest edge (BVB), 8♂, Quebec: Gatineau Co., Masham Twp, 11.vi.1974, D.M.Wood (BVB), 1♀, UNITED STATES: New Mexico: Catron Co., 2.4km W Luna, 7-8.vii.1987, B.V.Brown, yellow pans, 2300m, oak/ pine/ juniper (BVB); *A.* ***pergandei*** **Coquillett**, 1♀, CANADA: Ontario: Foote's Bay, shore of L.Joseph, 11-30.viii.1985, B.V.Brown, Malaise trap, 2nd growth deciduous forest (BVB); *A.* ***platypalpis*** **(Borgmeier)**, 1♂, 3♀, UNITED STATES: Arizona: Cochise Co., Coronado National Memorial, 11.viii.1984, B.V.Brown, blacklight (BVB); ***A. similis*** **Malloch**, 2♀, UNITED STATES: Arizona: Cochise Co., 18.5km W Portal, Basin Trail head, 8-10.vii.1987, yellow pans, B.Brown and T.Spanton, 1950m, oak/ pine/ juniper (BVB); *A.* ***tenuipes*** **Borgmeier**, 1♀, UNITED STATES: Florida: Putnam Co., Hollister, 26.iv.1985, E.G.Milstrey, emerged from puparium collected from gopher tortoise burrow (BVB); ***A. wallerae*** **Disney**, 2♀, UNITED STATES: Texas: Travis Co., Austin, University of Texas, Brackenridge Field Lab., 23.v.1980, D.Waller, with *Atta texana* (BVB); ***Apocephalus*** **new species 19 (near *wheeleri*)**, 1♂, 1 ♀ CANADA: Alberta: Opal, 53°59'N, 113°13'W, 23-24.v.1986, B.V.Brown, Malaise trap, sand, jackpine (BVB).

Material examined from other zoogeographic regions. Specimens of approximately 30 other species from the Neotropical Region were also examined, but most could not be identified with existing keys. The species that could be identified are the following: ***A. cultellatus*** **Borgmeier**, 19♀, ECUADOR: Pichincha: 17km E Santo Domingo, Tinalandia, 6-13.v.1987, B.V.Brown, 710m, clubhouse windows (BVB); ***A. laceyi*** **Disney**, 8♂, 13♀, ECUADOR: Napo: 10km SW Puerto Napo, Limon Chicta, 23-

27.v.1987, 600m, B.V.Brown, hovering above *Camponotus femoratus*, rain forest (BVB); ***A. paraponerae* Borgmeier**, approximately 100 specimens (males and females) from the following localities: COSTA RICA: Heredia: Puerto Viejo de la Sarapiquí, La Selva Biological Station, iv-v.1988, 1989, Malaise trap, on injured *Paraponera clavata*, B.V.Brown and D.H.Feener, rain forest, 40m (BVB), PANAMA: Canal Zone: Barro Colorado Island, [date?], D.H.Feener, on injured *Paraponera clavata* (BVB);

8.10.14 *Menozziola* Schmitz 1934b

Type species: *Apocephalus schmitzi* Menozzi 1921 (original designation by Schmitz (1927b) in description of subgenus *Apocephalus* (*Menozziola*))

Derivation of generic name. This genus is named after C. Menozzi, who described the type species.

Diagnosis. Anepisternum with long seta and many setulae. Abdominal constriction in female posterior to tergite 4. Tergite 5 and 6 extremely short; tergite 6 encircles entire segment. Female with lateral, setulose papilla on segment 5 or 6.

Way of life and immature stages. One european species, *M. schmitzi* (Mennozi), is a parasitoid of queens of the ant *Crematogaster scutellaris* (Olivier) (Menozzi, 1921) and of queens of the ant *Camponotus herculeanus* (Schmitz, 1934b). The life history of New World species is unknown.

Immature stages of *M. schmitzi* were described briefly by Schmitz (1934b).

Collecting methods. These flies are rarely collected in Malaise traps; baiting of host ants would be the preferable method of collecting them. One undescribed species from Florida (see material examined), was collected by brushing away debris at the opening of a *Peltotrupes* (Coleoptera: Scarabaeidae) burrow, and aspirating the flies as they left.

Geographic distribution. Species of this genus are known from Europe, Africa, North America and South America.

Phylogenetic relationships. This genus is the adelphotaxon of *Trucidophora* (Brown *et al.*, in press).

Hypothesized autapotypic character states of *Menozziola* include the following:

1 Anepisternum with long seta.

2 Female with setulose, lateral papilla on ovipositor.

Number of recognized species. Five, plus two undescribed Nearctic Region species.

Nearctic Region material examined. **Menozziola sp. 1**, UNITED STATES: Arizona: 1♀, Cochise Co., 12.5km S Sierra Vista, Ramsey Canyon, 9.vii.1987, B.V.Brown, Malaise trap, 1700m, oak/ pine/ juniper (BVB), ***Menozziola* sp. 2**, UNITED STATES: Florida: 1♀, Marion Co., Ocala National Forest, Juniper Springs, 19.xii.1985, B.Brown, *Peltotrupes* burrows (BVB).

8.10.15 *Trucidophora* Brown in press

Type species: *Styletta camponoti* Brown 1988 (original designation)

Derivation of generic name. From a Latin word meaning to kill cruelly, referring to the parasitic lifestyle of the type species.

Diagnosis. Wing vein R_{2+3} absent. Abdominal constriction in female posterior to tergite 4. Tergite 5 and 6 extremely short; tergite 6 encircles entire segment.

Way of life and immature stages. Adult females of *T. camponoti* seek out and parasitize queens of the ant genus *Camponotus* (Brown *et al.*, in press).

Immature stages were desribed by Brown *et al.* (in press).

Collecting methods. Adults of these flies are seen often around logs containing *Camponotus* colonies, and can be aspirated as they run or hover over the wood.

Immature stages can be collected by gathering alate female ants when they swarm.

Geographic distribution. Holarctic Regions

Phylogenetic relationships. This genus is the adelphotaxon of *Menozziola* (Brown *et al.*, in press).

Hypothesized autapotypic character states of *Trucidophora* include the following:

1 Wing vein R_{2+3} absent.

Number of included species. Total of two; one is found in the Nearctic Region.

Nearctic Region material examined. The material examined is listed in previous publications (Brown, 1988; Brown *et al.*, in press).

8.10.16 *Microselia* Schmitz 1934a

Type species: *Microselia rivierae* Schmitz 1934a (original designation)

Derivation of generic name. Unknown. See derivation of the generic name *Megaselia*.

Diagnosis. Frons with extra lower seta. Tarsomere 5 of foreleg of female pointed.

Way of life and immature stages. The Nearctic Region species *M. texana* was collected hovering over and attempting to oviposit on the ant *Paratrechina melanderi* Wheeler (D.H.Feener, personal communication), but also was found in association with other ants. Whether it is a parasitoid of many species of ants, or of only *Paratrechina*, is as yet unknown.

Immature stages are unknown.

Collecting methods. These flies are collected over disturbed colonies of their host ants, or over ants attracted to tuna baits. Occasionally, they are collected in Malaise and pan traps.

Geographic distribution. Africa, Europe, North and South America (but see phylogenetic relationships).

Phylogenetic relationships. At least the New World species of this genus are the adelphotaxon of *Pseudacteon*; thus the genus *Microselia* may be polyphyletic. Disney (1988) believes that the two New World species of this genus may not belong in a monophyletic group with the Old World species, and may instead be part of the genus *Pseudacteon*.

Hypothesized autapotypic character states of *Microselia* include the following:

1 Apical foretarsomere elongate, narrowed.

Number of recognized species. Total of eight; one is found in the Nearctic Region.

Nearctic Region material examined. ***M. texana*** **Disney**, UNITED STATES: **Arizona**: 1♀, Cochise Co., 5km W Portal, Sunny Flats Campground, 26.vii.1988, B.Brown and D.Feener, over *Aphaenogaster* (BVB).

8.10.17 ***Pseudacteon*** **Coquillett 1907**

Type species: *Pseudacteon crawfordi* Coquillett 1907 (original designation).

Derivation of generic name. Unknown. This name, which means "false Acteon", may refer to Acteon who was a hunter in Greek mythology.

Diagnosis. Frons with extra lower seta. Apical foretarsomere normal (not elongate, narrowed).

Way of life and immature stages. All species are parasitoids of ants, mostly of the genus *Solenopsis*. Feener (1987) observed the ovipositonal behavior of one species. Immature stages are unknown.

Collecting methods. Although these flies are collected occasionally in Malaise traps, they are collected most easily over disturbed colonies or baited workers of their host ants (for example Feener, 1987; Williams *et al.*, 1973).

Geographic distribution. Found worldwide.

Phylogenetic relationships. This genus is the adelphotaxon of New World species of *Microselia.*

Hypothesized autapotypic character states of *Pseudacteon* cannot be hypothesized at this time, until the relationships between this genus and *Microselia* have been clarified.

Number of recognized species. Total of thirty-nine; six are found in the Nearctic Region.

Nearctic Region material examined. ***P. antiguensis*** **(Malloch)**, BAHAMAS: 17♂, 10♀, San Salvador Island, 9-15.v.1982, D.Bowen (BVB), BARBADOS: Holetown, 2♂, 1♀, 22.iv., 2♀, 24.iv.1978, K.N.Barber, pan trap (BVB), COSTA RICA: Heredia: 2♂, 3♀, Puerto Viejo, La Selva, ii.1980, W.Mason (BVB), Limon: 2♀, Pandora, Estrella Valley, 28.iii.1984, G.V.Manley, Malaise trap (BVB), DOMINICAN REPUBLIC: 6♀, La Cambre, P.Plata, 380m, 21-24.iii.1978, L.Masner, Malaise trap (BVB), UNITED STATES: California: Riverside Co., 6♀, University of California, 7-21.vi.1983, D.Yu, Malaise trap (BVB); ***P. californiensis*** **Disney**, UNITED STATES: Arizona: 1♂, 26♀, Cochise Co., 18.5km W Portal, Basin Trail, 9.vii.1987, B.V.Brown, over *Liometopum occidentale luctuosum* (BVB); ***P. crawfordi*** **Coquillett**, MEXICO: Jalisco: 4♂, 4♀, Chamela, Building C, 27.vii.1984, D.H.Feener, #787, over *Solenopsis geminata* (BVB), TRINIDAD: 1♂, 2♀, Arima Valley, Simla Station, 2-10.vi.1977, Malaise trap, P.Feinsinger (BVB); ***P. curriei* (Malloch)**, CANADA: Alberta: 1♀, 15km SW Beaver Mines, Castle River Bridge Campground, 23-29.vii.1986, FIT, T.Spanton, spruce/ fir (BVB), British Columbia: 1♂, 6♀, Mt.Robson Provincial Park, 5.vii.-10.viii.1986, B.Brown and T.Spanton, FIT, 850m, cedar/ aspen/ pine (BVB), UNITED STATES: California: 1♀, Tuolumne Co., 13km NE Twain Hart, 15-26.vi.1986, FIT, B.Brown and T.Spanton, 1950m, montane forest (BVB); ***P. onyx* Steyskal**, UNITED STATES: Arizona: 1♀, Coconino Co., 7000', Coconino National Forest, 11 mi N Flagstaff, Bonito Park, mountain meadow, 7-8.viii.1984, carrion trap, L.B.Carlson (BVB), Cochise Co., 1♀, 18.5km W Portal, Basin Trail head, 8-10.vii.1987, yellow pans, B.Brown and T.Spanton, 1950m, oak/ pine/ juniper (BVB), 2♀, 14 km S Sierra Vista, Carr Cyn Road, 10-11.vi.1987, oak forest, B.V.Brown, yellow pans (BVB), 12.5km S Sierra Vista, Ramsey Canyon, 1♀, 13-23.vii.1986, 1♀, 29.vi.1987, B.V.Brown, Malaise trap, 1700m, oak/ pine/ juniper (BVB), California: 3♂, 6♀, Shasta Co., 1 km W Redding, 27-30.vi.1986, 200m, B.Brown and T.Spanton, FIT, manzanita/ oak (BVB).

Material examined from other zoogeographic regions. Many unidentified specimens from Costa Rica, Ecuador, Mexico, Panama, Peru, St.Kitts, Thailand, and Venezuela were examined.

8.10.18 *Myrmosicarius* Borgmeier 1928

Type species: *Myrmosicarius gracilipes* Borgmeier 1928 (original designation).

Derivation of generic name. This name is derived from the Greek word *myrmex* for ant, and the Latin *sicarius* for assassin, thus ant-assassin.

Diagnosis. Female with foretarsomeres partly fused, apical tarsomeres of at least foreleg, and in many species also the other legs, usually elongate, narrowed to point. Female with downward-curved, sclerotized ovipositor; tergite 7 with separate apical dorsal plate.

Way of life and immature stages. Most species are parasitoids of attine ants, namely *Atta* F. and *Acromyrmex* Mayr, but some have been collected with *Labidus praedator* (F.Smith) and *Solenopsis saevissima* F.Smith (Borgmeier, 1931).

The immature stages are unknown.

Collecting methods. Adults are rarely collected in Malaise traps, and should be searched for associated with host ants.

Geographical distribution. These flies are found in the New World only.

Phylogenetic relationships. This genus is the adelphotaxon of *Dacnophora*. Hypothesized synapotypic character states of these two genera include the following:

1 Tergite 7 with separate apical, dorsal plate.

2 Apical foretarsomere pointed, elongate.

Hypothesized autapotypic character states of *Myrmosicarius* include the following:

1 Ovipositor tube-shaped, curved downwards.

Number of recognized species. Total of twelve; one is found in the Nearctic Region.

Material examined. No specimens of the Nearctic Region species *M. texanus* Borgmeier were examined. Specimens examined from the Neotropical Region were as follows: ***M. persecutor* Borgmeier**, BRAZIL: Amazonas: Ilha de Marchantaria, Rio Solimoes, 3°15'S, 59°58'W, varzea, J.Adis, 1♀, 1.x.1981, 1♂, 22.i.1982 (INPA); ***Myrmosicarius* sp. 1**, COSTA RICA: 1♀, Braulio Carrillo National Park, 10°10'N, 84°07'W, 10.iv.1985, 500m, H.Goulet and L.Masner (BVB); ***Myrmosicarius* sp. 2**, VENEZUELA: Zulia: 1♀, 6km W La Concepcion, 18.vi.1976, A.S.Menke and D.Vincent (USNM).

8.10.19 *Dacnophora* Borgmeier 1961

Type species: *Dacnophora legionis* Borgmeier 1961 (original designation).

Derivation of generic name. This name is derived from a Greek word meaning to bite, apparently an euphemistic reference to the parasitic lifestye of species in this genus.

Diagnosis. Apical foretarsomere of female narrowed, elongate. Female ovipositor not tube-shaped (see Brown, 1988 for an illustration).

Way of life and immature stages. These flies are endoparasites of ants of the genera *Neivamyrmex* and *Labidus*.

Immature stages are unknown.

Collecting methods. Adults of *D. pectinatus* Brown are collected most easily using blacklight traps. The flies appear in the traps in the early evening. Other specimens have been collected over their ant hosts, in pan and Malaise traps.

Geographic distribution. These flies are found in the warm parts of the New World, sympatric with their ant hosts.

Phylogenetic relationships. This genus is the adelphotaxon of *Myrmosicarius*. Autapotypic character states cannot be hypothesized at this time, until relationships with *Myrmosicarius* are clarified.

Number of recognized species. Total of six; one is found in the Nearctic Region.

Nearctic Region material examined. ***D. pectinatus* Brown**, UNITED STATES: Arizona: 3♀, Santa Cruz Co., 16km N Nogales, Peña Blanca Lake, 28.vii.1988, B.Brown and D.Feener, blacklight (BVB).

Material from other zoogeographic regions. ***D. legionis*** **Borgmeier,** ECUADOR: Pichincha: 1♀, 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown and L.Coote, Malaise trap, rain forest, 180m (BVB); ***Dacnophora*** **sp.1,** COSTA RICA: Puntarenas: 1♀, Monteverde, 1500m, 29.ii.1980, Mason and Wood, cloud forest (BVB).

8.10.20 *Neodohrniphora* **Malloch 1910a**

Type species: *Neodohrniphora calverti* Malloch 1910a (original designation)

Derivation of generic name. This name is derived from the supposed similarity between this genus and *Dohrniphora* Dahl.

Diagnosis. A diagnosis of this genus is difficult to construct, as the included species probably do not form a monophyletic taxon. Most of the useful character states are negative, for instance, apical foretarsomere not narrowed. Borgmeier (1966) gives a diagnosis that is probably accurate but not extremely useful. See below (phylogenetic relationships).

Way of life and immature stages. All species for which life history data are available are parasitoids of leaf-cutting ants of the genera *Acromyrmex* and *Atta*, with the exception of *N. arnaudi*, for which a host is unknown, and that occurs outside the range of any species of leaf-cutting ant (Feener & Moss, 1990). The behavior of one species, *N. curvinervis* (Malloch) was observed at the La Selva Biological Station, Puerto Viejo de la Sarapiquí, Heredia Province, Costa Rica (Feener & Brown, in manuscript). Individual females wait on perches (leaves, branches) over columns of workers of *Atta cephalotes* (author?) until an outward-bound worker of suitable size comes into range. The fly leaves its perch and flies along the ant-trail, hovering over its intended victim, attempting to oviposit. Successful oviposition apparently occurs when the fly is able to land on the back of the ant's head, facing forward, insert the tip of its ovipositor through the occipital foramen and deposit an egg inside the head. Intended ant victims flee when they notice a phorid stalking them and attempt to dislodge ovipositing females.

The immature stages of *N. curvinervis* (Malloch) will be described by Brown and Feener (in preparation).

Collecting methods. Adult specimens of *Neodorhniphora* can be collected by aspirating them from over their ant hosts.

Geographic distribution. The species of this genus are found in the New World only, with most found in the Neotropical Region.

Phylogenetic relationships. The relationships of this genus and possible autapotypic character states are unknown. Unfortunately, this genus is not well defined, and may contain more than one monophyletic lineage. The type species of *Neodohrniphora* is also the type of one of the two species groups proposed by Prado (1976): the *N. calverti*-group and the *N. curvinervis*-group. The members of the *N. calverti*-group are definitely related to the genus *Cremersia*, as they share the presence of a small hook-shaped seta on the female ovipositor. The relationships of *N. curvinervis*-group species and *N. arnaudi* Borgmeier are less clear; these may not belong in a monophyletic group with *N. calverti*-group taxa.

Number of included species. Total of eight; one is found in the Nearctic Region.

Nearctic Region material examined. ***N. arnaudi*** **Borgmeier**, CANADA: British Columbia: 1♂, 1♀, North shore of Shuswap Lake, 50°59'N, 119°06'W, 23-31.viii.1987, 400m, J.E.O'Hara, Malaise trap, columbian forest (BVB), UNITED STATES: Arizona: Cochise Co., 18.5km W Portal, Basin Trail head, 9♂, 1♀, 7-10.vi.1986, B.V.Brown, Malaise trap, 1♂, 8-10.vii.1987, B.Brown and T.Spanton, yellow pans, 1950m, oak/ pine/ juniper (BVB), 1♂, near Portal, S.W.R.S., 10.vi.1965, V.Roth, Malaise trap (BVB), 1♂, 12.5km S Sierra Vista, Ramsey Canyon, 9.vii.1987, B.V.Brown, Malaise trap, 1700m, oak/ pine/ juniper (BVB), California: 3♂, 2♀, Tuolumne Co., 13km NE Twain Hart, 15-26.vi.1986, FIT, B.Brown and T.Spanton, 1950m, montane forest (BVB), New Mexico: Catron Co., 2.4km W Luna, 2300m, 5♂, 3♀, 7-8.vii.1987, B.V.Brown, yellow pans, 2♂, 1♀, 7.vii.1987, T.G.Spanton, Ponderosa pine/ oak/

juniper forest (BVB).

Material examined from other zoogeographic regions. Note: most Neotropical Region specimen in my collection cannot be identified with the existing treatment (Prado 1976). ***Neodohrniphora*** **sp. 1**, ECUADOR: Napo: Tena, 1♂, 10♀, 20-27.v.1987, 500m, B.V.Brown, hovering above *Atta cephalotes*, 1♀, 15.ii.1986, A.T.Finnamore, sweep (BVB); ***Neodohrniphora*** **sp. 2**, ECUADOR: Napo: 1♀, 5km N El Chaco, 15.ii.1983, M.Sharkey, Malaise trap (BVB); ***Neodohrniphora*** **sp. 3**, COSTA RICA: Heredia: La Selva Biological Station, 40m, 3♀, ii.1980, W.Mason, 20♂, 16-26.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50, 1♀, 23-26.v.1988, B.V.Brown, Malaise trap, 2° forest, SAT 100, 1♀, 21.iv.1989, B.Brown and D.Feener, over *Atta cephalotes*, study colony (BVB), Puntarenas: 14♀, Corcovado National Park, Sirena, 3.vi.1987, D.H.Feener, over *Atta cephalotes* (BVB); ***Neodohrniphora*** **sp. 4**, MEXICO: Jalisco: Chamela, Chachalaca Trail, 3♀, 9.vi.1984, #0685, 19♀, 26.vii.1984, #0786, 35♀, 27.vii.1984, #0788, D.H.Feener, over *Atta mexicana* (BVB); ***Neodohrniphora*** **sp. 5**, COSTA RICA: Heredia: 3♂, 2♀, La Selva Biological Station, 40m, 23-26.v.1988, B.V.Brown, Malaise trap, 1° forest, SSO 50 (BVB); ***Neodohrniphora*** **sp. 6**, ECUADOR: Pichincha: 3♀, 1♂, 47km S Santo Domingo, Rio Palenque Science Center, 29.iv.-5.v.1987, B.Brown and L.Coote, Malaise trap, rain forest, 180m (BVB). Also, unidentified male specimens were examined from Costa Rica, Ecuador, Mexico and Venezuela.

8.10.21 *Cremersia* Schmitz 1924

Type species: *Cremersia zikani* Schmitz 1924 (original designation).

Derivation of generic name. This name was proposed by Schmitz for his friend J.Cremers (Schmitz, 1924).

Diagnosis. Wing vein R_{2+3} reduced, faint. Female terminalia extremely complicated, asymmetrical. Male terminalia extremely asymmetrical, right side of epandrium extremely reduced.

Way of life and immature stages. These flies are endoparasites of New World army ants of the genera *Eciton*, *Labidus*, *Neivamyrmex* and *Nomamyrmex*.

Immature stages are unknown.

Collecting methods. Adults can be collected as they hover over the host ants. Specimens are also encountered in Malaise and blacklight traps.

Geographic distribution. These flies are found in the warm parts of the New World, sympatric with their ant hosts.

Phylogenetic relationships. This genus is the adelphotaxon of at least some species of *Neodohrniphora*. See above (Phylogenetic relationships of *Neodohrinphora*) for more details.

Hypothesized autapotypic character states of *Cremersia* include the following:

1 Many character states associated with the asymmetrical and extremely complicated female terminalia.

2 Right side of epandrium reduced.

Number of recognized species. Total of fourteen; three are found in the Nearctic Region.

Nearctic Region material examined. ***Cremersia* sp.1**, UNITED STATES: Arizona: 1♂, 1♀, Cochise Co., 12.5km S Sierra Vista, Ramsey Canyon, 9.vii.1987, B.V.Brown, Malaise trap, 1700m, oak/ pine/ juniper (BVB).

Material examined from other zoogeographic regions. Specimens of several undescribed species were examined from Costa Rica, Ecuador, Panama, Peru, and Venezuela.

8.10.22 ***Auxanommatidia* Borgmeier 1924**

Type species: *Auxanommatidia variegata* Borgmeier 1924 (original designation).

Derivation of generic name. This name is derived from a Greek word meaning to increase or grow, and ommatidia, or eye fascicles, referring to the increasing size of these structures in the ventral part of the eye.

Diagnosis. Frons narrowed anteriorly. Ommatidia enlarged ventrally.

Way of life and immature stages. These flies are parasitoids, with one species recorded as attacking *Camponotus* (Borgmeier, 1925).

Collecting methods. These flies are occassionally collected in Malaise traps, but should be searched for on their host ants.

Geographic distribution. Known from the New World and Africa.

Phylogenetic relationships. Unknown. The diagnosis of this genus is unsatisfactory, and the included species need to be studied closely. Autapotypic character states cannot be hypothesized at this time.

Number of included species. Total of ten; two are found in the Nearctic Region. Borgmeier (1968, 1971) was apparently unaware of the description of *A. boreotis* Beyer (1963).

Nearctic Region material examined. ***A. californica*** **Borgmeier**, CANADA: Alberta:

1♀, Opal, 53°59'N, 113°13'W, 15-22.vii.1986, B.V.Brown, Malaise trap, sand, jackpine (BVB), British Columbia: 2♂, 1♀, north shore of Shuswap Lake, 50°59'N, 119°06'W, 23-31.viii.1987, 400m, J.E.O'Hara, Malaise trap, columbian forest (BVB), UNITED STATES: California: 1♀, Sierra Co., Salmon Creek Campground, 8km NE Sierra City, 1768m, 5.vii.1975, P.H.Arnaud, Jr. (BVB), 1♀, Siskiyou county, McBride Springs, 7.viii.1967, 1524m, P.H.Arnaud, Jr. (BVB), 1♂, Tuolumne Co., 6km NE Tuolumne, River Ranch Campground, 22-26.vi.1986, B.V.Brown, Malaise trap, oak forest/ field, 750m (BVB).

8.10.23 *Zyziphora* Peterson and Robinson 1976

Type species: *Zyziphora hirutifrons* Peterson and Robinson 1976 (original designation).

Derivation of generic name. This name is based on an arbitrary combination of letters, according to the original description.

Diagnosis. Only female known. Frons with 8-10 pairs of supra-antennal setae.

Way of life and immature stages. Unknown. The single specimen was collected from cow dung, but is probably a parasitoid.

Collecting methods. Unknown.

Geographic distribution. Known only from the type locality in Colorado, USA.

Phylogenetic relationships. Unknown. This species may be the female of *Anticofimbria* Schmitz, known from Japan.

Hypothesized autapotypic character states of *Zyziphora* include the following:

1 Frons with 8-10 pairs of supra-antennal setae.

Number of recognized species. Only one, the type species, found in the Nearctic Region.

Nearctic Region material examined. None.

8.11 Conclusions and suggested future work

The relationships of the Metopininae are far from being understood satifactorily. Within the relatively primitive lineages, all members of the former taxon Beckerinini must be examined to determine their placement in the system. The relationships of the *Metopina*-group genera are unknown, and must be revised on a world scale. The relationships of the the *Megaselia*-group genera have been worked out partially, but within the *Apocephalus*-series, many genera are considered only tenuously monophyletic. Adelphotaxon relationships among pairs of these genera invariably involve one genus that cannot be defined without also including the other, relatively more derived genus; the included species of these taxa must be revised. The paraphyletic genus *Megaselia* must be organized into monophyletic units, which remains a daunting task. Progress will only be made on these problem areas when species level revisions are made of their component genera.

8.12 Acknowledgements

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Table 8.1. Distribution of plesiotypic and synapotypic character states among the basal genera and genera-groups of Metopininae. 0 - plesiotypic, 1 - synapotypic, ? - equivocal or unknown.

Characters	12345678901
Taxa	
Triphleba	10000000000
Rhopica	?110?000000
Beckerina	?1111110000
Megaselia-group	11011111100
Metopina-group	11011111011

Table 8.2. Distribution of plesiotypic and synapotypic character states among the *Megaselia*-group genera and genera-groups. 0 - plesiotypic, 1 - synapotypic, ? - equivocal or unknown.

Characters	1234567890123
Taxa	
Pericyclocera	1000000000000
Trophithauma	1000000000000
Megaselia (in part)	1000000000000
Gymnophora	1100000000000
Woodiphora	1100000000000
Megaselia (in part)	1100000000000
Diocophora	1010000000000
Kerophora	1010000000000
Myriophora	1010000000000
Phalacrotophora	1011000000000
Rhyncophoromyia	1011000000000
Physoptera	1011000000000
Apocephalus	1010110000000
Lecanocerus	0010110000000
Auxanommatidia	0010110000000
Zyziphora	?010110000000
Trucidophora	0010111110000
Menozziola	0010111110000
Pseudacteon	0010110001000
Microselia	0010110001100
Dacnophora	0010110000110
Myrmosicarius	0010110000110
Cremersia	0010110000101
Neodohrniphora	0010110000001

Fig. 8.1. A, *Gymnophora luteiventris* Schmitz, thorax, lateral; B-D, *Apocephalus* sp., B, abdomen, posterodorsal; C, ovipositor, lateral; D, ovipositor, ventral; E, *G. luteiventris*, female abdomen, dorsal; F, *Myriophora* sp., apex of ovipositor, left lateral. Abbreviations: a - aperture of segment 7, i - intersegment 6/7, nc - notopleural cleft, s7, s8 - sternite 7, 8, t7, t8 - tergite 7, 8.

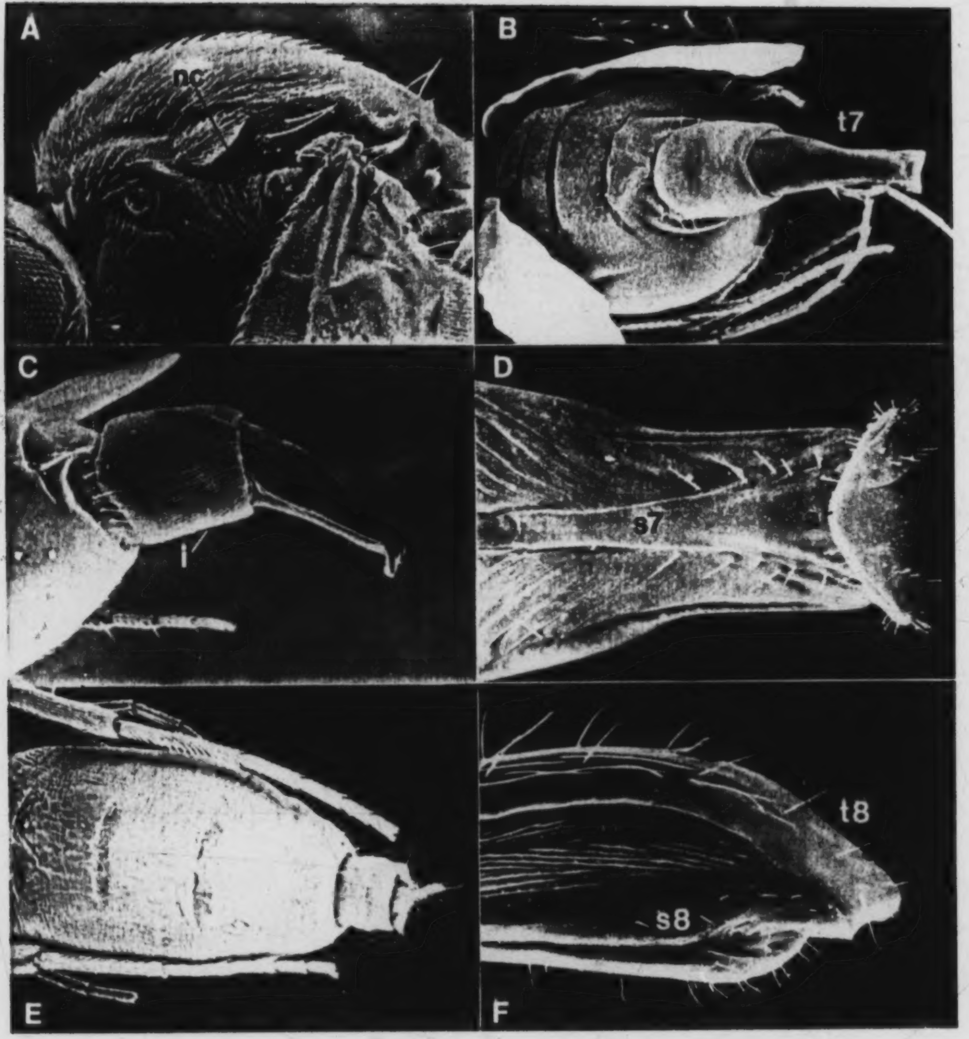

A
nc
B
t7
C
l
D
s7
E
F
t8
s8

Fig. 8.2. Dufour's mechanisms. A, *Megaselia aequalis* (Wood); B, *M. cavernicola* (Brues); C, *Megaselia* sp.; D, *Megaselia* sp.; E, *Pseudohypocera kerteszi* (Enderlein); F, *Pericyclocera* sp.; G, *Kerophora* sp.; H, *K. ferruginea* Brown; I, *Myriophora* sp. 2; J, *Physoptera membranosa* Borgmeier; K, *Diocophora appretiata* Schmitz; L, *Rhycophoromyia* sp. 3; M, *Apocephalus paraponerae* Borgmeier; N, *A. antennatus* Malloch. Scale bar = 0.1mm, all figures to same scale.

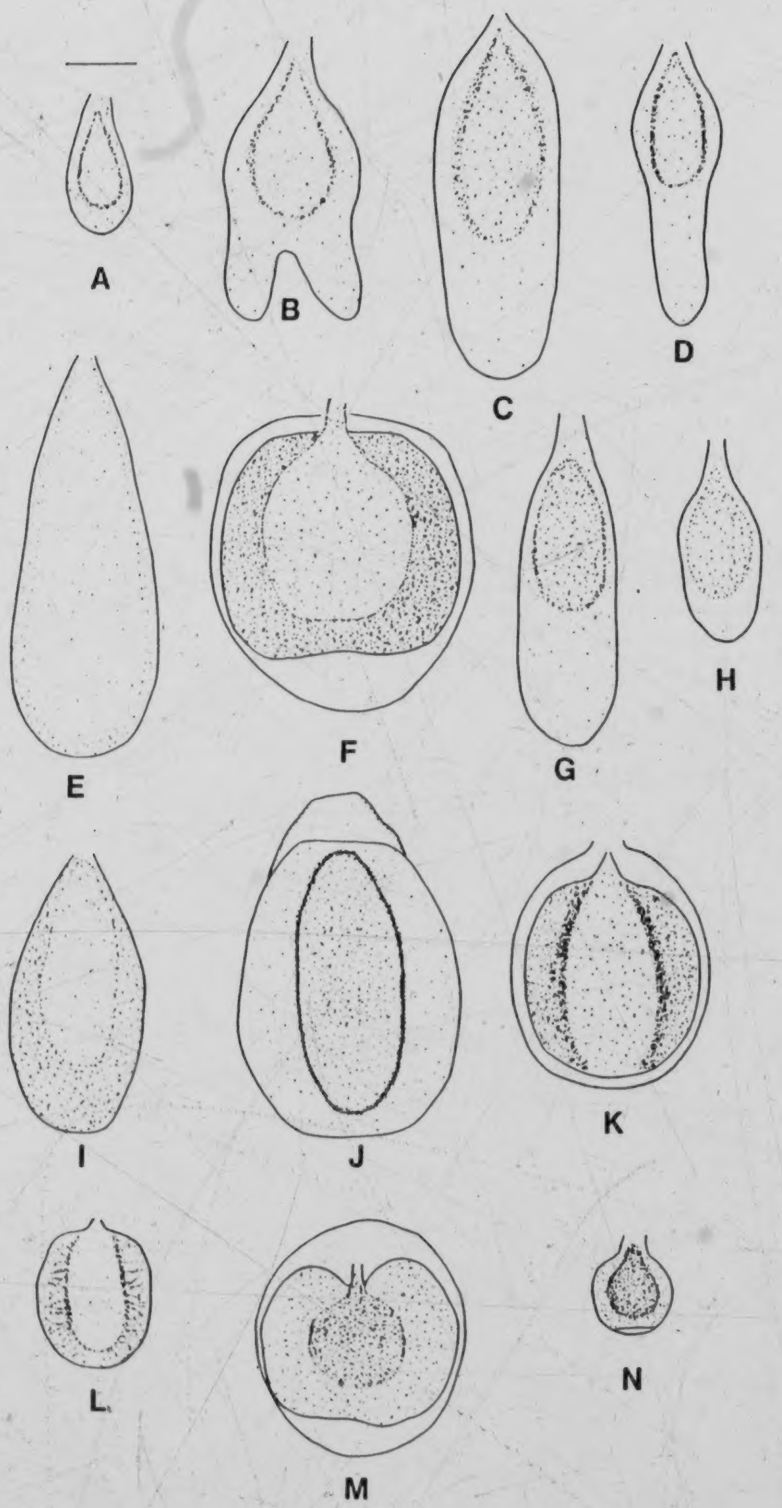

A
B
C
D
E
F
G
H
I
J
K
L
M
N

Fig. 8.3. A, *Megaselia* sp., tip of ovipositor, dorsal; B-E, male terminalia. B, *Aphiura breviceps* Schmitz; C, *Corynusa latifrons* (Schmitz); D, *Exochaeta umbrata* Schmitz; E, *Macroselia* sp.; F, *Metopina* sp., male terminalia, right lateral. Scale bar = 0.1mm, Figs. A-E to same scale. Abbreviations: e - epandrium, h - hypandrium, u - u-shaped tergite.

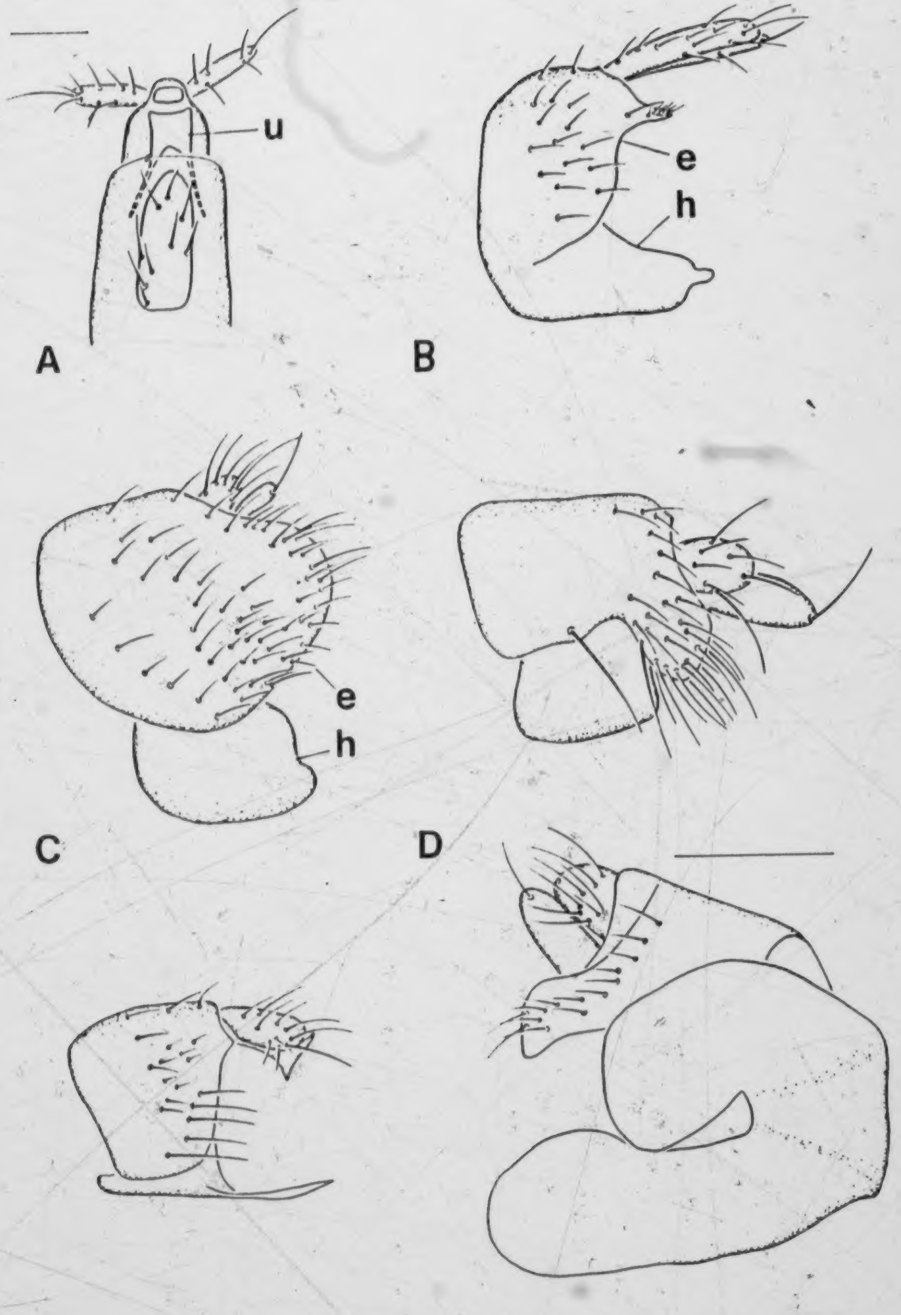

u
e
h
A
B
e
h
C
D
E
F

Fig. 8.4. *Myriophora* sp. 3, apex of female ovipositor, right lateral, cerci extruded. Scale bar = 0.1 mm. Abbreviations: c - cercus, e - epiproct, h - hypoproct, s8 - sternite 8, t8 - tergite 8.

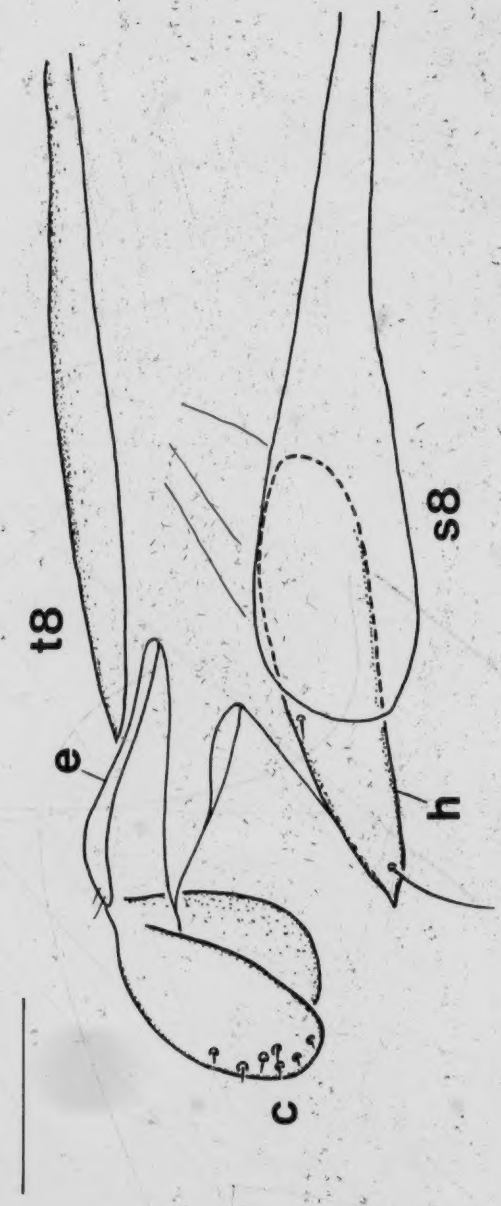
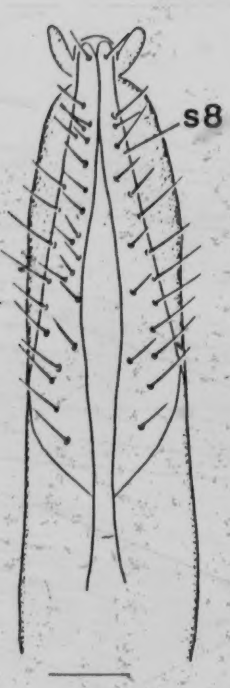
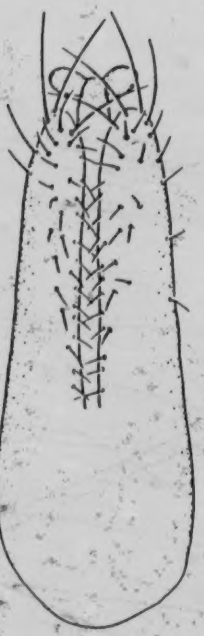

♀
t8
s8
e
h
c

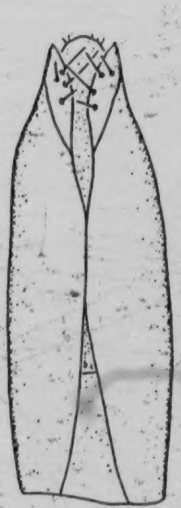
Fig. 8.5. Female terminalia, ventral. A, *Phalacrotophora* sp.; B, *Physoptera membranosa* Borgmeier; C, *Rhyncophoromyia conica* (Malloch). Scale bar = 0.1mm, all figures to same scale. Abbreviation: s8 - sternite 8.



A



B



C

Fig. 8.6. Hypothesized relationships of the Metopininae. Character states in parentheses are reversals.

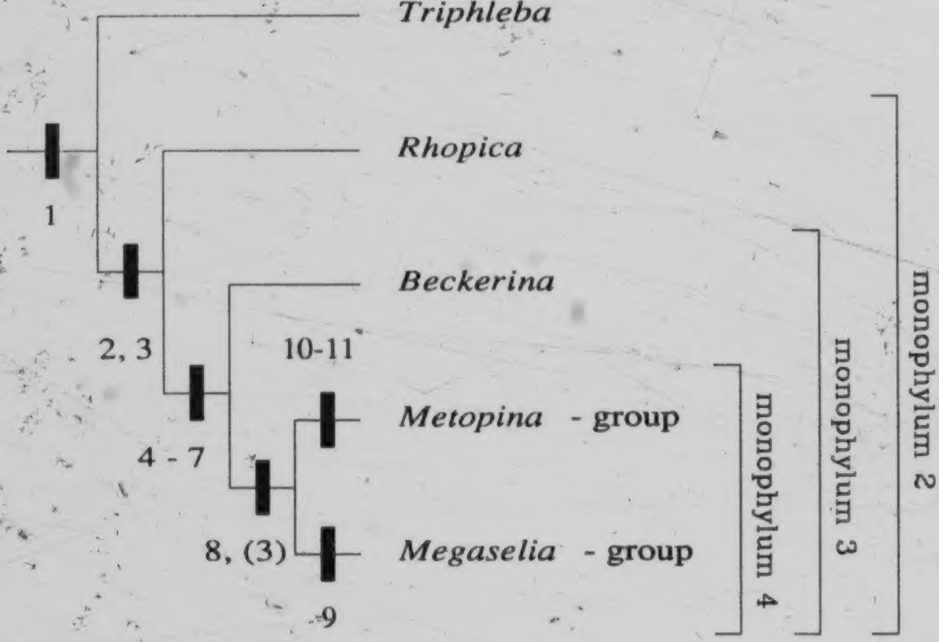

Triphleba
Rhopica
Beckerina
Metopina - group
Megaselia - group
1
2, 3
4 - 7
8, (3)
10-11
9
monophylum 2
monophylum 3
monophylum 4

Fig. 8.7. A, Cladogram given by Disney (1989a); B, Disney's cladogram redrawn. Numbered synapotypies are those of Disney (1989a).

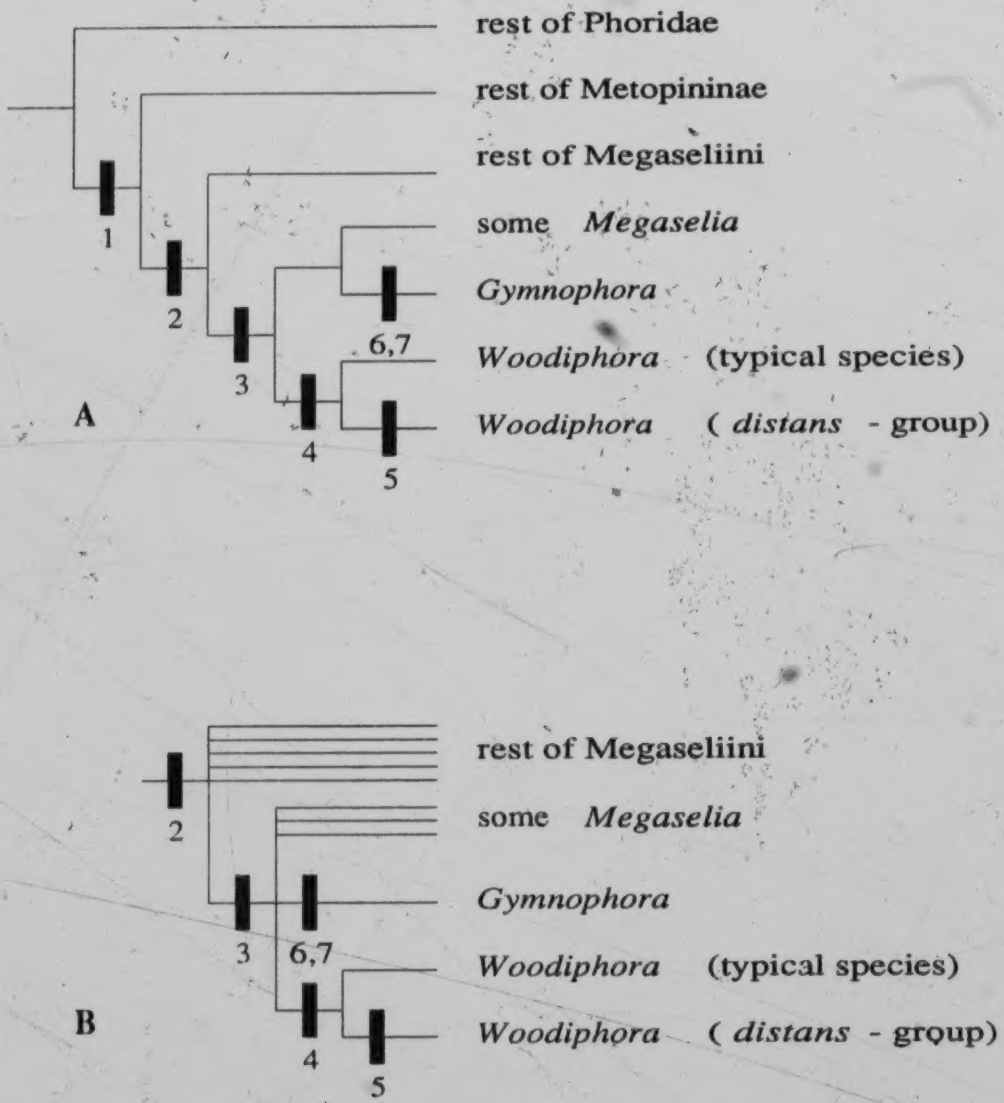

rest of Phoridae
rest of Metopininae
rest of Megaseliini
some *Megaselia*
Gymnophora
Woodiphora (typical species)
Woodiphora (*distans* - group)
1
2
3
6,7
4
5
A
rest of Megaseliini
some *Megaselia*
Gymnophora
Woodiphora (typical species)
Woodiphora (*distans* - group)
2
3
6,7
4
5
B

Fig. 8.8. Hypothesized relationships of the *Megaselia*-group.

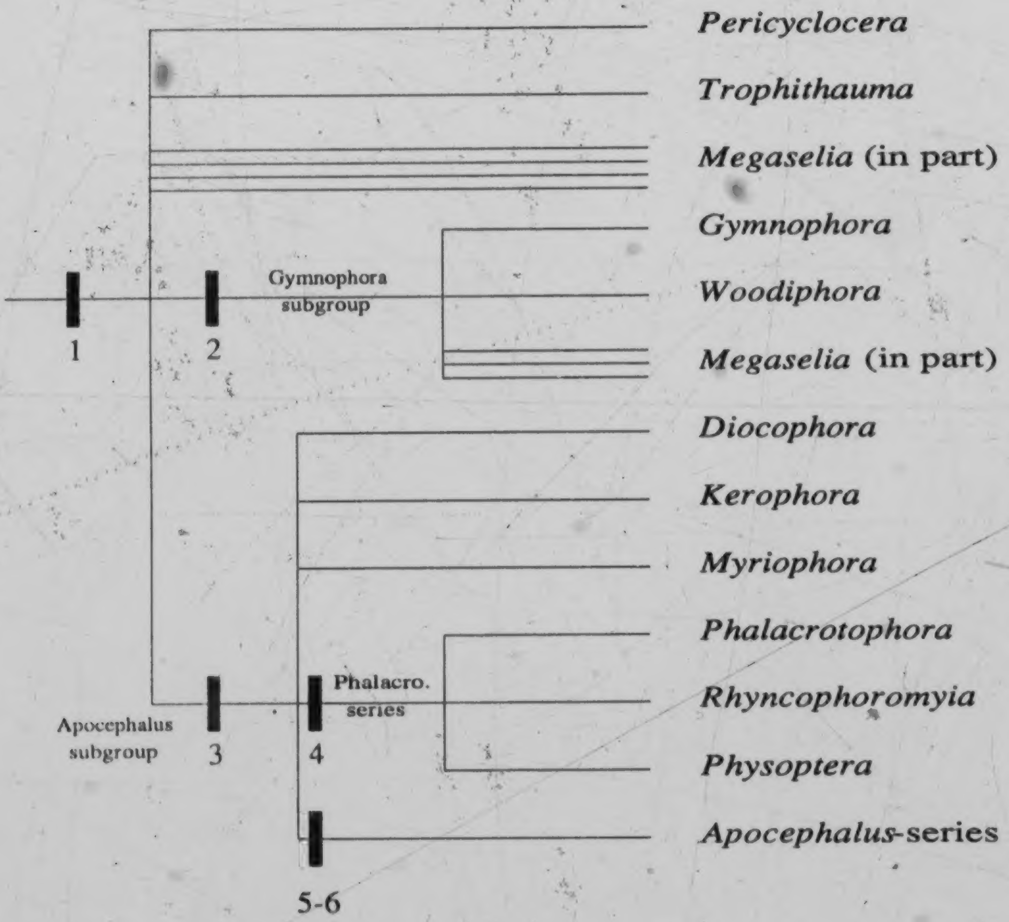
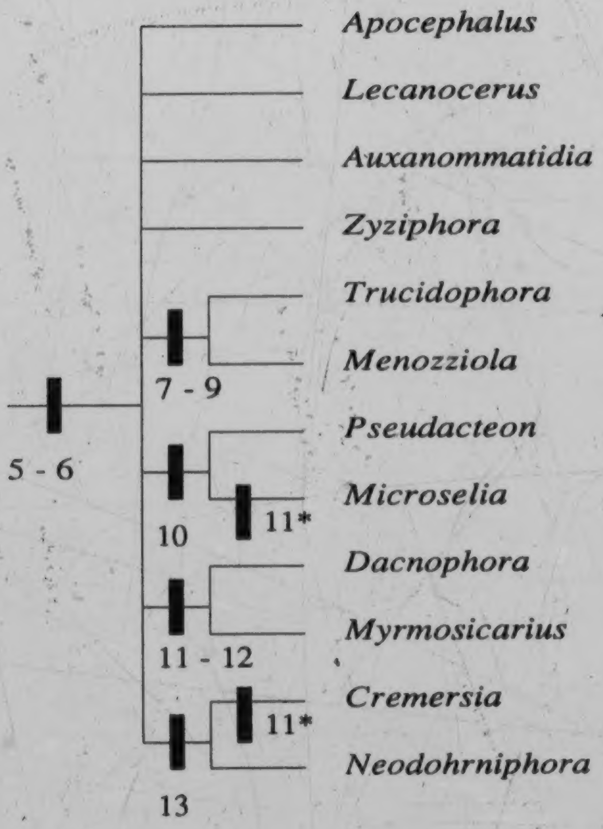

Pericyclocera
Trophithauma
Megaselia (in part)
Gymnophora
Woodiphora
Megaselia (in part)
Diocophora
Kerophora
Myriophora
Phalacrotophora
Rhyncophoromyia
Physoptera
Apocephalus-series
1
2
Gymnophora subgroup
Apocephalus subgroup
3
4
Phalacro. series
5-6

Fig. 8.9. Hypothesized relationships of the *Apocephalus*-series. Character states with asterisks are homoplastic.


Apocephalus
Lecanocerus
Auxanommatidia
Zyziphora
Trucidophora
Menozziola
Pseudacteon
Microselia
Dacnophora
Myrmosicarius
Cremersia
Neodohrniphora
5 - 6
7 - 9
10
11*
11 - 12
11*
13

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9. CONCLUSIONS

9.1 Evolutionary trends within the Phoridae

It is clear from the revision presented above that there are character states and trends that appear repeatedly throughout the Phoridae. These trends represent parallel evolution, or underlying synapotypies as described by Saether (1979), and present problems in classification and character analysis.

One distinct evolutionary trend is the reduction of wings in adult females and development of what Borgmeier called degenerate females. These flies are further characterized by the loss of halteres, reduction in size of body setae, reduction in size of tergites, and loss of the scutellum. Such females are present in all phorid subfamilies, and examples include females of *Billotia* Schmitz (Hypocerinae, see Appendix 1), *Rhychomicropteron* Annandale (Phorinae, see Appendix 1), *Diplonevra gynaptera* Fuller and Lee (Aenigmatiinae, tribe Diplonevrini), most members of Aenigmatiinae, tribe Aenigmatiini, *Contopteryx* Schmitz (Conicerinae) and most members of the *Metopina*-group of genera (Metopininae). The reduced structures of these degenerate females may be adaptations to an exclusively terrestrial existence, where wings, halteres, long setae, *etc.* would be an impediment to free movement through small interstices and tangled vegetation. Furthermore, many of these flies are associated with social insects, living in the nests of ants and termites. Reduction of projecting body structures is important to prevent an attacking host insect from gaining a hold on the body surface. In many instances these characters are further modified in myrmecophilous and termitophilous phorids, producing limuloid females, like those of Aenigmatiini. Limuloid females have a distinctive teardrop-shape, are rounded, depressed, and have heads that are tightly pressed against the prothorax, all character states that further protect these insects from attack. Such females are found in *Rhychomicropteron* (Phorinae, see Appendix 1), Aenigmatiini, and Metopininae (Brown, submitted). Males are seldom brachypterous or wingless, except in a few taxa found on mountaintops (for example *Gymnophora lapidicola* (Bezzi) and some undescribed species of *Megaselia* from Nepal). In many species, winged males transport wingless or brachypterous females to new breeding sites, while mating in flight (Brown, 1986; Edwards & Schmitz, 1939; Gotô, 1983; Miller, 1984; Schmitz, 1933).

Other prominent trends occur in the life histories of phorids. One such tendency is towards myrmecophily and termitophily, as discussed above. Another is the trend towards a parasitic lifestyle. Generally, it is assumed that the ancestral way of life in phorids is saprophagy (Oldroyd, 1964; Rohdendorf, 1974), but outgroup information is lacking. The only outgroup taxon with a known life history is *Sciadocera rufomaculata* White, which breeds in decaying meat (H. Oliver, personal communication). The female ovipositors of *Ironomyia nigromaculata* White (McAlpine, 1967), *Archiphora patagonica* (Schmitz) (Chapter 2) and *Sciadophora bostoni* McAlpine and Martin (1966) are pointed and modified, those of at least the last two apparently for parasitism. The life histories of hypocerines, the relatively most primitive phorid lineage are almost completely unknown, except for parasitism by species of *Peromitra* Enderlein and possibly by *Stichillus* Enderlein. Larvae of the phorines are scavengers (*Anevrina* Brues, *Chaetopleurophora* Schmitz, *Coniceromyia* Borgmeier, *Rhychomicropteron* Annandale, *Spiniphora* Malloch) or predators (*Phora* Latreille). Immatures of various aenigmatiine taxa are scavengers (*Dohrniphora* Dahl, some species of *Diplonevra* Lioy), or parasitoids (*Aenigmatias* Meinert, some *Diplonevra*, *Misotermes* Schmitz), but the life histories of most species are unknown. Some conicerines are scavengers (*Conicera* Meigen, *Gymnoptera* Lioy) as are some species of primitive-grade Metopininae (*Triphleba* spp.). Species of many *Metopina*-group genera are scavengers, but within some genera there may be taxa that are parasites and saprophages (Disney, 1988) and species of some genera are predators. The *Megaselia*-group contains the largest number of parasitic species, with the entire *Apocephalus*-subgroup having this lifestyle. Larvae of other *Megaselia*-group taxa are saprophages, parasites or predators.

Thus, although parasitism is widespread (found in Hypocerinae, Aenigmatiinae, and Metopininae) the evolution of this way of life remains a mystery. Presumably, saprophagy is the primitive way of life, and the opportunity to exploit living tissue has arisen many times. An example of this series of events may be furnished by *Apocephalus paraponerae* and other parasites that attack wounded ant hosts. The ancestors of such a lineage could have bred in recently killed ants, but selective pressure to develop as quickly as possible in the rapidly decomposing food item may have led to attacking ants closer and closer to the point of death. Eventually, ants were attacked before their death, when only injured. Today, *A. paraponerae* attacks its hosts merely when they are disturbed and emitting their alarm pheromone as well as when injured, the next step towards true parasitism (Brown & Feener, in press). Adults of other species of *Apocephalus* attack readily non-injured ants (eg. Feener, 1981, 1987, 1988; Feener & Brown, submitted; Feener & Moss, 1990), the final stage in this progression. It should be noted that this hypothesized sequence of events has not been verified by demonstrating that *A. paraponerae* is structurally a relatively primitive species; such verification can occur only after the species of the genus *Apocephalus* are revised.

9.2 Zoogeographic considerations

In general, little can be said about the zoogeography of the Phoridae based on this revision. Certainly areas like Australia and New Zealand, which have large numbers of relatively primitive mammals, birds, reptiles, etc., have also large numbers of relatively primitive phorids. Conversely, areas like the Neotropical Region that have had large, relatively recent radiations of birds and mammals, also have had radiations of relatively derived phorids, such as *Apocephalus*-series genera, which are absent from New Zealand. The presently restricted ranges of many relatively primitive phorid groups are undoubtedly the result of recent extinctions. A Dominican amber fossil specimen of *Antipodiphora* Schmitz and Canadian late Cretaceous and Baltic amber fossils of Sciadoceridae are examples of taxa once more widespread but now restricted to New Zealand (*Antipodiphora*), or Australia, New Zealand and south Chile. Samples of Phoridae from Madagascar, an area expected to have extremely primitive taxa, are disappointing in their lack of diversity and their general similarity to African faunas. Apparently, phorids are able to travel over large bodies of water, probably carried by storms or steady winds, and to colonize islands fairly easily. Thus, the apparent antiquity of the New Zealand fauna could be because of survival of early immigrants from other regions. Otherwise, the age of phorids on New Zealand must be hypothesized to be much older than any fossil evidence for Cyclorrhapha, representing the survival of a relictual fauna from the late Jurassic vicariance events associated with the breakup of the southern hemisphere continents.

9.3 General conclusions

The logical precursor to organizing the Phoridae is looking to its outgroup, or most closely related taxa, for guidance. The outgroup for the Phoridae is believed to be the families Sciadoceridae and Ironomyiidae, but Disney has decided to re-assess all knowledge about phorids and their relatives. This has caused him to take a radical view of all relationships, and he has challenged the monophyly of the Phoroidea, the group containing the Phoridae, Sciadoceridae and Ironomyiidae. As I have shown in Chapter 2, however, this challenge is not well based, and does not counter successfully the well-supported hypotheses of relationship among these families.

Within the Phoridae itself, six subfamilies were recognized by Schmitz: Phorinae, Aenigmatiinae, Metopininae, Thaumatoxeninae, Termitoxeniinae and Alamirinae. Of these, the last three occur only in Old World tropical termite nests and do not concern this study. Of the first three subfamilies, it was the Phorinae that caused the greatest problem, since this subfamily was defined on primitive characters only. Willi Hennig, the father of phylogenetic systematics, considered the Phorinae to be probably paraphyletic (Hennig, 1973), but Chapter 3 contains the first real evidence to support this idea. The undoubted placement of *Triphleba* Rondani with the other metopinines showed that the Phorinae was indeed paraphyletic, and the character states defining the group had to be re-examined.

The next group that I recognized was one that Schmitz was well aware of sixty years ago, which he referred to as the *Borophaga*-group of genera. This newly proposed subfamily, the Hypocerinae, is one of the best supported groups in the family, and numerous character states found in the male terminalia of its component taxa allow reconstruction of generic relationships.

The Phorinae is a less satisfactory group. This name formerly referred to all primitive phorids, but its new, more restricted use is reserved for genera with a distinctive, presumed dorsal-ventral clasping mechanism in the male terminalia. The wide range of character states found in the genus *Chaetopleurophora* Schmitz, however, make analysis of this subfamily difficult, and the relationships remain largely unknown.

The Aenigmatiinae is a distinctive group of flies with flattened, cockroach-like females that seemed to have little in common with any other living phorid groups, and I despaired of ever finding a place for them in my system. Discovery of the remarkable female of *Synaptophora critica*, new genus, new species, from Africa, however, showed that this group has at least three character states in common with the *Diplonevra*-group of genera. The female of *S. critica* is in all respects like the type genus of Aenigmatiinae, *Aenigmatias* Meinert, except that it has fully developed wings, large setae on the tibiae and frons, and distinctive lateral sclerites on segments 7 and 8. This last character state, found also in species of *Diplonevra* Lioy and *Dohrniphora* Dahl, made me realize that these groups belonged together in an expanded concept of the Aenigmatiinae.

The Conicerinae includes several genera that have long, pointed male antennae. This character state is not uncommon in other phorid lineages such as in some species of *Coniceromyia* Borgmeier and some *Metopina*-group genera. The conicerine genera all belong at the same grade of evolution, however, and their relationships seem to be soundly established.

The Metopininae, with its new member taxon *Triphleba*, is the most strongly supported group within the Phoridae. The divided anepisternum found in adults is a character state unknown elsewhere in the Phoroidea, and thus constitutes a relative rarity in the family: an example of a primary synapotypy, apparently not subject to homoplasy. Within the Metopininae, the picture is less clear, with a number of taxa formerly placed in the paraphyletic tribe Beckerinini having uncertain relationships around the base of the subfamily, and numerous genera of the *Metopina*-group and

Megaselia-group with uncertain relationships within their respective groups. Here, I was able to improve only slightly on the relationships proposed by Disney (1989) for *Megaselia*-group genera.

Having come full-circle to face my original thesis project, a re-organization of *Megaselia*, I find that there is some improvement in the classification of closely related genera, but much more work is needed. In the subfamily Metopininae, the genera *Megaselia* and *Apocephalus* Coquillett need species-level revision. The full range of character states within these genera must be determined before their constituent taxa can organized into monophyletic groups. The revision of *Megaselia* is vital to understanding the generic relationships of the relatively more primitive *Megaselia*-group genera, whereas the relationships of *Apocephalus* species are necessary to understand the *Apocephalus*-series genera, many of which are characterized inadequately.

Within other subfamilies, the genera in greatest need of revision are *Peromitra* Enderlein in the Hypocerinae, and *Chaetopleurophora* in the Phorinae. The definition of *Peromitra* is far from satisfactory, and the included species in fact may be a paraphyletic assemblage that is ancestral to the relatively more derived genus *Stichillus* Enderlein. The problems with the genus *Chaetopleurophora* have been discussed above.

Now that the phorid genera have been re-organized, I believe that the time has come to concentrate on species-level revisionary work to provide the raw data for the next re-classification of the family. Unlike Schmitz, however, who died in 1960, I hope that I do not have to wait until the year of my death for the next revisor to be born.

9.4 References

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Appendix 1

Genera of primitive grade phorids not included in this revision

Besides the genera of tribe Aenigmatiini (Aenigmatiinae), the following genera were not examined or not placed in the phylogenetic system I have proposed. Some of these have since been placed, based on material recently examined.

Billotia **Schmitz 1944**

This genus belongs to the subfamily Hypocerinae.

Brachyselia Schmitz 1927

I examined no specimens of this genus.

Gymnoselia Schmitz 1927

I examined no specimens of this genus.

Kierania **Schmitz 1939**

I examined one male of this genus. It appears to belong to the same grade as the subfamily Phorinae, as it has a separate right surstylus. The hypandrium, however, is not extensively modified, and the right process is only slightly longer than the left. In the absence of any better evidence to link this genus with other phorines, I leave it unclassified.

Kuenbergia Schmitz 1937

This genus is known from females only, so its relationships cannot be hypothesized at this time. I examined no specimens of this genus.

Obscuriphora Disney 1986

Disney stated that this genus was close to *Plethysmochaeta* (Phorinae), but gave no synapotypic character states to support this conclusion. I examined no specimens of this genus.

Postoptica Disney 1987

It is unknown to which subfamily this genus belongs. Disney declined to place it in any of the existing subfamilies, but it is clear at least that *Postoptica* does not belong to the Metopininae. I examined no specimens of this genus.

***Rhynchomicropteron* Annandale 1912**

Males of this genus have terminalia like members of the subfamily Phorinae, but I have not studied enough material to be sure that they belong at this level. The females are similar to members of the tribe Aenigmatiini (subfamily Aenigmatiinae), although they were originally placed in the subfamily Metopininae (Disney, 1981; Schmitz, 1929). If this genus does belong in the subfamily Phorinae, then this is the third lineage of limuloid, aenigmatiine-like phorids (the others being tribe Aenigmatiini and the *Melittophora*-group of Metopininae, Brown, submitted).

Syneura Brues 1903

Species of this genus are similar to species of *Megaselia*-group genera, but have neither a Dufour's mechanism nor a parasitic-type ovipositor. For now, they must remain unclassified.

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Appendix 2. Abstracts of papers in this thesis

Outgroups and some ground pattern character states of Phoridae (Diptera).

ABSTRACT. The relationships of the families Ironomyiidae, Sciadoceridae and Phoridae are reviewed, showing that the prevailing theory about their relationships are probably correct. Sciadoceridae and Phoridae are more closely related to each other than to Ironomyiidae. The male terminalia of the newly re-collected *Archiphora patagonica* (Schmitz), as well as those of *Sciadocera rufomaculata* White show that separate surstyli are present in both genera. The holotypes of the fossil phorids *Sciadophora bostoni* McAlpine and Martin and *Prioriphora canadambra* McAlpine and Martin are re-examined, and compared with other recently described Cretaceous Phoridae, showing that this group is part of the stem lineage of the Phoridae. A revised phylogeny of the group is presented that is identical to a previous model, but is supported by some different character states.

Groundpattern character states and subfamily classification of Nearctic Region Phoridae (Diptera)

ABSTRACT. The Nearctic Region phorid genera are organized into five subfamilies: Hypocerinae, Phorinae, Aenigmatiinae, Conicerinae and Metopininae. The Hypocerinae includes *Abaristophora* Schmitz, *Borophaga* Enderlein, *Burmophora* Beyer, *Hypocera* Lioy and *Stichillus* Enderlein. The genus name *Crinophleba* Borgmeier is a synonym of *Burmophora* (**syn. n.**), with the affected taxa being *B. angustifrons* (Gotô) (Japan), *B. rostrata* (Borgmeier) (Canada) and *B. vitrinervis* (Malloch), all **comb. n.** The newly re-defined Phorinae includes *Anevrina* Lioy, *Chaetopleurophora* Schmitz, *Coniceromyia* Borgmeier, *Phora* Latreille and *Spiniphora* Malloch. The Aenigmatiinae is organized into two tribes: Aenigmatiini, including the genus *Aenigmatias* Meinert, and *Diplonevrini*, including *Diplonevra* Lioy, *Dohrniphora* Dahl and *Hypocerides* Schmitz. *Synaptophora critica* **gen. n., sp. n.**, a phylogenetically important member of tribe Aenigmatiini, is described from a single female from Uganda. The Conicerinae includes genus *Conicera* Meigen. The Metopininae includes all genera traditionally placed in this subfamily, plus the former phorine taxa *Mannheimsia* Beyer, *Phlebothrix* Borgmeier, and *Triphleba* Rondani. The metopinine tribe Beckerinini is shown to be paraphyletic, and the tribe Megaseliini is ranked too high. Hypocerinae is the adelphotaxon (=sister-group) of other phorids, whereas Phorinae is the adelphotaxon of Aenigmatiinae + Conicerinae + Metopininae, among which the relationships are unknown.

Revision and phylogenetic classification of the genera of Hypocerinae (Diptera: Phoridae).

ABSTRACT. The subfamily Hypocerinae Lioy contains those phorid genera, previously contained in the paraphyletic subfamily Phorinae, which have outwardly-directed hypandrial lobes and basally curved wing vein M_1. Included taxa are *Abaristophora* Schmitz (Holarctic Region), *Antipodiphora* Schmitz (New Zealand), *Borophaga* Enderlein (Holarctic Region), *Bothroprosopa* Schmitz (New Zealand), *Burmophora* Beyer (Holarctic and Oriental Regions), *Ceratoplatus* Schmitz (New Zealand), *Godavaria* new genus (Oriental Region), *Hypocera* Lioy (Holarctic and Oriental Regions), *Latiborophaga* new genus (Afrotropical and Neotropical Regions), *Palpocrates* Schmitz (New Zealand), *Peromitra* Enderlein (Palearctic and Oriental Regions), *Stichillus* Enderlein (widespread), *Tarsocrates* Schmitz (New Zealand), *Tonnoiriphora* new genus (New Zealand), and *Trineurocephala* Schmitz (Neotropical Region). *Godavaria* **new genus** is proposed for the type species *G. setulosa* **new species**, from Godavari, Nepal, plus the following **new combinations**: *G. eminens* (Beyer) (Burma), *G. inflata* (Beyer) (Burma), *G. minor* (Beyer) (Burma and Thailand) and *B. orientalis* (Beyer) (Burma). *Latiborophaga* **new genus** is proposed for the type species *L. pachycostalis* (Borgmeier) (Neotropical Region), *L. insignis* (Borgmeier & Prado) (Neotropical Region), *L. rufibasis* (Beyer) (Afrotropical Region) and *L. simia* (Beyer) (Afrotropical Region), all **new combinations**. *Tonnoiriphora* **new genus** is

proposed for New Zealand taxa previously classified in *Triphleba*, subgenus *Tonnoirina*; the affected taxa are *T. atripalpis* (Schmitz), *T. fuscithorax* (Schmitz), and the type species *T. rufithorax* (Schmitz), all **new combinations**. Species of *Borophaga*, subgenus *Peromitra* Enderlein are found to be more closely related to species of *Stichillus* and *Trineurocephala* than to other *Borophaga* and thus the name is elevated to generic status (**new status**); affected taxa are *Peromitra agilis* (Meigen) (Europe), *P. carinifrons* (Zetterstedt) (Europe), *P. cephalotes* (Schmitz) (Europe), *P. erythrocera* (Meigen) (Europe), *P. eumimeta* (Beyer) (Burma), the type species *P. incrassata* (Meigen) (Europe), *P. multisetalis* (Colyer) (USSR), and *P. subagilis* Beyer (Burma) (all **new combinations**); species classified as *Borophaga* (*Borophaga*) belonging in *Peromitra* include *P. amurensis* (Schmitz) (Siberia), *P. cornigera* (Beyer) (Burma), and *P. germanica* (Schmitz) (Europe), all **new combinations**. The phylogenetic relationships were determined as follows: two major monophlyletic groups are the *Stichillus*-subgroup (*Peromitra*, *Stichillus*, and *Trineurocephala*) and the *Borophaga*-subgroup (*Abaristophora*, *Antipodiphora*, *Borophaga*, *Godavaria*, and *Latiborophaga*), which together form the *Borophaga*-group; *Hypocera* is the adelphotaxon (=sistergroup) of the *Borophaga*-group, *Bothroprosopa* is the adelphotaxon of *Hypocera* + *Borophaga*-group, and *Palpocrates*, *Tarsocrates* and *Tonnoiriphora* form an unresolved polytomy near the base of the subfamily. *Burmophora* is the adelphotaxon of all other hypocerines. Within the *Stichillus*-subgroup, the relationships are unknown. Within the *Borophaga*-subgroup, *Abaristophora* and *Antipodiphora* are adelphotaxa, and are organized into the *Abaristophora*- series, but their relationships to

Borophaga, *Godavaria*, and *Latiborophaga* are unknown. The relationships of *Ceratoplatus* are unknown at this time.

Revision and phylogenetic classification of the Nearctic Region genera of the subfamily Phorinae (Diptera: Phoridae)

ABSTRACT. The newly re-defined subfamily Phorinae includes the following Nearctic Region genera: *Anevrina* Lioy, *Chaetopleurophora* Schmitz, *Coniceromyia* Borgmeier, *Phora* Latreille and *Spiniphora* Malloch. The genus *Plethysmochaeta* Schmitz (not Nearctic) also belongs in this group. Adelphotaxa (sister-groups) include *Chaetopleurophora* + *Spiniphora*, and *Coniceromyia* + *Phora*. The relationships between other genera are unknown. The Phorinae is defined by a distinctive, presumed clasping, mechanism in the male terminalia.

Revision and phylogenetic classification of the genus *Aenigmatias* Meinert 1890 (tribe Aenigmatiini), and of the genera of tribe Diplonevrini (Diptera: Phoridae: Aenigmatiinae)

ABSTRACT. The Nearctic region genera of the subfamily Aenigmatiinae are revised, including members of the newly proposed tribes Aenigmatiini and Diplonevrini. The Aenigmatiini contains the type genus *Aenigmatias* Meinert (Holarctic Region) and many other genera previously recognized as Aenigmatiinae. The Nearctic Region Diplonevrini are *Hypocerides* Schmitz, *Diplonevra* Lioy, and *Dohrniphora* Dahl, all of which are found worldwide. Diplonevrini from other zoogeographical regions are *Aenictomyia* Brues (Philippines), *Dicranopteron* Schmitz (Java), *Multinevra* Disney (Africa, Oriental Region), and *Myopiomyia* Disney (Sulawesi). Males of the Diplonevrini have a constriction of the epandrium apically, near the cercus, that results in a neomorphic, separate sclerite in some species of *Diplonevra*. Within the Diplonevrini are the *Hypocerides*-group, including *Hypocerides* and *Multinevra*, and the *Diplonevra*-group, including *Diplonevra* and the *Dohrniphora*- subgroup (*Aenictomyia*, *Dicranopteron*, *Dohrniphora*). The genera *Multinevra* and *Hypocerides* are tentatively considered adelphotaxa (=sistergroups), but freshly collected female specimens of both genera are needed to resolve this satifactorily. The genus *Apopteromyia* Beyer (Australia) is synonymized with *Diplonevra*. The generic relationships within the Aenigmatiini were not examined on a world basis.

Revision and phylogenetic classification of genera of subfamily Conicerinae (Diptera: Phoridae)

ABSTRACT. The world genera of Conicerinae include *Ceratusa* Borgmeier (Neotropical Region), *Cyphometopis* Borgmeier (Neotropical Region), *Gymnoptera* Lioy (widespread), *Contopteryx* Schmitz (southern South America), *Darwiniphora* Schmitz (southern South America), and *Conicera* Meigen (widespread). *Conicera* and *Darwiniphora* are adelphotaxa (sister-groups) and probably should be represented by one generic name only. *Contopteryx* is the adelphotaxon of *Conicera* + *Darwiniphora*, and *Gymnoptera* is the adelphotaxon of *Contopteryx* + *Conicera* + *Darwiniphora*. *Ceratusa* and *Cyphometopis* are probably a single lineage, and probably should have one generic name; they are the adelphotaxa of all other conicerines. Male terminalia of all genera except *Cyphometopis* are illustrated.

Subfamily Metopininae: diagnoses and phylogenetic classification of genus-groups, and revision of genera of the Nearctic Region (Diptera: Phoridae).

ABSTRACT. Revision of the Nearctic Region metopinine genera shows that there are two major groups, the *Megaselia*-group and the *Metopina*-group. *Beckerina* Malloch is the adelphotaxon (sister-group) of the these two groups, whereas *Rhopica* Schmitz (not Nearctic) and *Triphleba* Rondani are successively more distant adelphotaxa. Within the *Megaselia*-group are the *Gymnophora*-subgroup, including *Gymnophora* Macquart, *Woodiphora* Schmitz, and some species currently classified in *Megaselia* Rondani, the *Apocephalus*-subgroup, and three unassigned taxa: *Trophithauma* Schmitz, *Pericyclocera* Schmitz, and the paraphyletic assemblage *Megaselia*. Within the *Apocephalus*-subgroup are *Diocophora* Borgmeier, *Kerophora* Brown, *Myriophora* **gen. n.**, the *Phalacrotophora*-series, including *Phalacrotophora* Enderlein, *Rhyncophoromyia* Malloch, and *Physoptera* Borgmeier, and the *Apocephalus*-series. *Myriophora* contains some species formerly classified as *Plastophora* Brues and *Megaselia*, the affected taxa being *M. audreyae* (Disney), *M. elongata* (Wood), *M. equitans* (Schmitz) and the type species *M. juli* (Brues); all are **comb. n.** and all known species are parasites of myriapods. The *Apocephalus*-series contains a large number of parasitic genera, many of which have lost the Dufour's mechanism, the defining trait of the *Megaselia*-group. The relationships between the *Apocephalus*-

series genera are not well understood. The relationships of the *Metopina*-group genera were not examined.

Vita

I was born in Toronto, Ontario, Canada, on 16 November 1960, 76 days after the death of my entomological hero, Hermann Schmitz. Growing up in and around Toronto, I gained an early interest in insects and appreciation for conservation while exploring abandoned farms and vacant lots that would soon become suburban developments. I obtained my Bachelor of Science and Master of Science degrees in 1983 and 1985 at the University of Guelph, Ontario, with the encouragement and support of Dr. Steven A. Marshall, who rescued me from brief diversions into aquatic crustaceans and a semi-professional rock and roll band. Since that time, my professional interests have not diverged substantially, and in 1986 I made my way to Alberta to continue my studies on Phoridae. My current interests center around the systematics of ant-attacking phorids, especially of tropical regions.